Status of Forest Regeneration in Dieback Affected *Abies densa* (Eastern Himalayan Fir) Stands of Chamgang-Helela region (Thimphu), Western Bhutan.

Thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science in Mountain Forestry

at

University of Natural Resources and Applied Life Sciences, (BOKU), Vienna.

Supervisor:

Em. O. Univ. Prof. DI Dr. Gerhard Glatzel

Co-Supervisor:

Ao. Univ. Prof. DI Dr. Georg Gratzer

Submitted by:

Sonam Tobgay

June, 2009

DEDICATIONS

To

My Daughter

Whose presence in my life gives a whole new meaning and beginning to my life

To

My Parents, Wife, Brothers, Sister, Uncle, Aunt & In-laws

For their unconditional love, support, encouragement and understanding through out my life and tolerating my absence for a long time

ACKNOWLEDGEMENTS

This study was conducted in partial fulfillment of the requirement for the degree of Master of Science in Mountain Forestry and funded by ÖAD, Austrain Development Agency. I am extremely grateful to my scientific supervisior, Em. O. Univ. Prof. DI Dr. Glatzel Gerhard and co-supervisor, Ao. Univ. Prof. DI Dr. Gratzer Georg for providing necessary guidance and supervision from the conception until the completion of my thesis. Their patience and consideration for helping me even during odd hours is highly appreciated. I am sincerely grateful to DI Dr. Andras Darabant for his valuable help, suggestions during the initial part of my data analysis and Nawang Gyeltshen,NBC for the entire field work, both of them equally deserve to be mentioned for the successful completion of my thesis. I am also thankful to Mr. Martin Wresowar for providing technical support and being kind enough to share his room during the thesis work and Ms. Melanie for her help, support and understanding during the entire period especially in regard to my appointments with my supervisor.

I remain ever grateful to my former Program Director / NBC, Dr. Ugyen Tshewang for my nomination and the present Program Director, Dr. Tashi Yangzom for her administrative support and cooperation during my field work in Bhutan. I thank my wife Dechen Lham, Botanical Garden and Mr. Tandin Wangdi, National Herbarium, NBC for the logistics support and sparing their staff for my field work.

Special thanks also go to Dr. Pema Wangda, P.B. Rai, Dorji, RNR-RC for their guidance and cooperation during initial field work. At the same time I appreciate and thank the following personnel of NBC for their help and cooperation:

Sangay Khandu, Norbu Rabling, Sangay Lungten, Dupchu Wangdi, Santa Gurung, Pema, Kezang Tshering, Bir Bahadur Gurung.

Lastly, my heartfelt thanks to my Sollingergasse friends (Sangay, Rinzin, T Penjor, Nawang, Nagdrel, Kinley, Loja, Dimple, Sigyel and Purna); my classmates and other Austrain friends whose companionship and understanding made my stay in Vienna a lively and a memorable one.

ABSTRACT

In the sub-alpine, natural mono-specific A*bies densa* forests in Chamgang-Helela region, Thimphu (Western Bhutan), almost all trees in the upper ridges were killed by drought triggered massive fir dieback in the late 1970s and early 80s. There is lack of information regarding the regeneration and vegetation dynamics of these affected fir stands. We investigated tree regeneration in 20 20x20m randomly established permanent plots spread across the study area with a distance of 50m between each plot. Inside each plot 5 1x1m mini-plots were nested. The working hypothesis was that ultimately die-back affected stands would be replaced again by mono-specific *Abies densa* stands, because fir, with the exception of *Juniperus recurva*, is the only dominant, long lived tree species at this elevation. Some advanced tree regeneration was present in the vicinity of the mini-plots but not inside the mini-plots. Since the dieback *Abies* seeds have been deposited and germinated, although recruitment during the initial years after the dieback was discontinuous. At present an average density of 0.6 seedlings of fir per m^{-2} exists. The fact that only 26 percent of the mini-plots showed regeneration indicates patchiness of the regeneration which will result in a mosaic of dense and open forest. Different site factors and other factors like micro-site (moss, leaf litter, mineral soil and organic matter), grazing, shade, slope, altitude, competing ground vegetation have influence on *Abies densa* germination and survival. The mortality of *Abies densa* germinants could not be observed. The seedling density of other tree and shrub species like *Juniperus recurva* (0.1 m^{-2}), *Acer sp.* (0.18 m^{-2}), *Rhododendron arboreum* (0.13 m^{-2}), *R. cinnabarinum* (0.11 m^{-2}), *R. lepidotum* (0.18 m^{-2}), *R barbatum* (0.02 m^{-2}), *Viburnum nervosum* (0.01 m^{-2}) and *Rosa sericea* (0.29 m m^{-2}), were much lower compared to *Abies densa* (0.6 m-²). These low numbers indicate that it is unlikely that a closed pioneer, *Juniper* or *Acer* stand will be formed, displacing the previous fir stands. For some time, the forest stands will be a mosaic of dense and wide spaced fir trees. We anticipate that over time, mono-specific *Abies densa* forest will eventually once again replace the present stand composition of the dieback affected fir stands.

Keywords: Forest regeneration, disturbance, forest die-back, micro-sites, *Abies densa*, replacement

KURZFASSUNG

In den subalpinen Reinbeständen von *Abies densa* tarben in den späten 1979er und frühen 1980iger Jahren fast alle Bäume auf den höheren Bergrücken infolge eines durch eine extreme Klimafluktuation ausgelösten Waldsterbens ab. Über den gegenwärtigen Zustand der betroffenen Bestände ist wenig bekannt. Daher wurden in einem ausgewählten Gebiet zwanzig 20x20 m Versuchsflächen angelegt um den Zustand und die Verjüngungsdynamik zu studieren. Innerhalb der Probeflächen dienten je 5 1x1m Mini-Plots der Untersuchung von Sämlingen von Bäumen und der krautigen Vegetation. Die Arbeitshypothese war, dass die abgestorbenen Bestände letztendlich wieder durch Tannenreinbestände ersetzt würden, weil die Tannedie einzige langlebige dominante Baumart in dieser Höhenlage ist. Es zeigte sich, dass einige Bäume das Waldsterben überlebt haben und nun als fortgeschrittene Verjüngung in der Umgebung von Mini-Plots vorhanden sind. Innerhalb der Mini-Plots war dies allerdings nicht der Fall. Nach dem Absterben wurden Tannensamen eingetragen und sind auch gekeimt. Gegenwärtig beträgt die Tannenverjüngung über alle Flächen gemittelt 0.6 Individuen je m^{-2}. Die Tatsache, dass Tannenverjüngung nur in 26 Prozent der Mini-Plots zu finden war, zeigt die unregelmäßige Verteilung. Die Korrelation mit verschiedenen Einflussfaktoren wie Standortsbedingungen oder Nähe zu Migrationswegen von Weidevieh zeigte signifikante Einflüsse auf die Tannenverjüngung. Die Verjüngungsdichte anderer Holzgewächse wie *Juniperus recurva* (0.1 m-^{2}), *Acer sp.* (0.18 m-^{2}), *Rhododendron arboreum* (0.13 m-^{2}), *R. cinnabarinum* (0.11 m-^{2}), *R. lepidotum* (0.18 m-^{2}), *R barbatum* (0.02 m-^{2}), *Viburnum nervosum* (0.01 m-^{2}) und *Rosa sericea* (0.29 m-^{2}), war im Vergleich zuo *Abies densa* (0.6 m-^{2}) viel niedriger. Jungpflanzen von Pioniergehölzen wie *Betula utilis, Sorbus foliolosa* fehlten oder waren sehr rar (*Salix sp.*, 0.02 m-^{2}). Diese Ergebnisse zeigen, dass eine Entwicklungsphase aus geschlossenen Beständen anderer Baumarten und insbesondere von Pioniergehölzen, unwahrscheinlich ist. Es ist anzunehmen, dass letztendlich wieder Tannenreinbestände den Platz der abgestorbenen Bestände einnehmen. Allerdings wird über lange Zeit ein Mosaik aus geschlossenen und eher offenen Bereichen den Wald prägen.

Stichworte: *Abies densa*, Waldseterben, Bhutan, Verjüngung, Dyanamik

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX

Glossary

Dzongkhag	District
Tsamdrog	Registered forest land for cattle grazing
Chhu	River

Abbreviations

m	meter
cm	centimeter
sq.km	square kilometer
masl	meters above sea level
m^2	meter square
ha^{-1}	per hectare
ha	hectare
DBH	Diameter at breast height
RGoB	Royal Government of Bhutan
F&NC Act	Forest and Nature Conservation Act
LUPP	Landuse Planning Project
RNR-RC	Renewable Natural Resource-Research Centre
FMU	Forest Management Unit
NBC	National Biodiversity Centre
FRDD	Forest Resources Development Division
DoF	Department of Forests
MoA	Ministry of Agriculture
IFMP	Integrated Forest Management Project

1 INTRODUCTION

In the late 1970s and early 1980s sub-alpine fir forest stands (*Abies densa* Griff.) of Western Bhutan were affected by widespread dieback problems (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994). Stand-level dieback has been reported from many forest types around the world (Mueller-Dombois 1991). Regeneration and development of forest starts from a disturbance (Yamamoto, 1992b; Runkle, 1998; in Nagaike, T., 2003). Since then no new dieback episode is reported and affected stands seem to recover slowly. There is an obvious lack of information on the regeneration dynamics in the affected fir stands. Therefore a selected site in a severely damaged fir forest in the Chamgang-Helela region under Thimphu district was investigated for post dieback vegetation dynamics.

As Bhutan is a small, landlocked and densely forested Himalayan country in the South East Asia (FAO 1999, 2001 in Kirisits *et al.*, 2007), forests are of great importance for the ecological, economical, social well being of the country and the livelihood of its people. In Bhutan, the temperate conifer forests form the natural vegetation in mountainous places at elevations from 2,100 upto 4,200masl and occupy about 24% of the total land area of the country. Conifer forests occupy about 24% of the total land area of the country (Grierson-Long, 1983; in Rosset, 1999). The East Himalayan Fir (*Abies densa* Griff.) forests occupy 11% (3, 453 sq.km) of the area of Bhutan (LUPP 1995) and occur at altitudes between about 3,000 to 4,000masl (Donaubauer, 1994).

However almost three decades after the massive fir dieback in western Bhutan, no studies have been conducted till date to study and understand the post dieback regeneration structure and dynamics of these dieback affected forest stands of western Bhutan. A mosaic of patches created by gap formation mainly affects stand structure and regeneration (Nakamura, 1985 in Nagaike, 2003). Few studies were conducted in central Bhutan on fir regeneration and it was reported (McKinnon 1995, Dhital, 1998 in Gratzer *et al.*, 2002) that the structure and dynamics of these forests are poorly understood and documented which poses problems for both sustainable forest management and nature conservation. It is clear that there is lack of information available on vegetation dynamics or on the succession patterns following the stand level breakdown. Multiple scale analysis of forest structure and regeneration will allow to identify the driving factors for forest dynamics particularly in areas where no information on the disturbance regime is available and information on autecological characteristics of trees is very less (Pabst and Spies, 1999 in Gratzer *et al.*, 2002).

Photo 1: The dieback affected fir forest on the upper ridges of sub-alpine level in summer 2008 from the lower limit of the dieback affected stands (Source: Sonam Tobgay)

It is reported (Allen and Rose, 1983), that as a result of dieback, major changes occur in the structure and composition of the affected stands. Stand structure is influenced by disturbance through modification of external environment (White & Pickett, 1985; Fujihara *et al.*, 2000). It is therefore the aim of this study to examine the post dieback regeneration structure and dynamics of these dieback affected fir stands and identify main factors influencing vegetation recovery after the dieback. At the same time we intend to determine whether the stands will be replaced by fir or displaced with other tree species.

It is reported (Franklin and Forman, 1987; Harris, 1984; in Zheng *et al.* 1997) that implementation of landscape change and conservation area design conceptual models starts within a description of current landscape patterns and trends. Analysis of present patterns of forests offers a present day baseline for assessing future landscape patterns and their consequences. However, to better understand the process of forest development post-dieback that has shaped the current stand structure, it is necessary to quantify the regeneration and determine the main factors driving the recovery of the stand. This would be useful for developing better future resource management strategies and for determining future landscape changes.

2 LITERATURE REVIEW

2.1 The Fir Dieback of the late 1970s and early 1980s in Western Bhutan

In the late 1970s and early 1980s, conifer forests of Western Bhutan were affected by widespread fir (*Abies densa* Griff.) dieback problems (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994) and bark beetle outbreak i.e. *Ips schmutzenhoferi* on Spruce (*Picea spinulosa*) and Bluepine (*Pinus wallichiana*) and *Ips longifolia* on Chirpine (*Pinus roxburghii*) (Schmutzenhofer 1987a, 1987b, 1988; Holzschuh, 1988; Tshering-Chhetri, 2000; Kirisits *et al.*, 2002 in Kirisits *et al*, 2007). Firs at their ecological optimum forms single tree species stands over large areas i.e. mono-specific which regenerate from single tree gaps formed by breakage of severely rotten trees (Gratzer *et al.*, 1997). The decline was restricted to the upper elevations of fir zone and at lower elevations only on single trees or smaller groups the decline was observed. These two large scale forest health problems have for the first time shown that diseases, insect pests and abiotic agents can pose immense threat to Bhutan’s forests and greatly upset aims of forest management and conservation (Kirisits *et al*, 2007). Fir dieback or decline is the most important health problem of fir forests in Bhutan (Donaubauer 1986, 1987, 1993; Ciesla and Donaubauer, 1994) where many fir stands over extensive areas were affected and at many places large portions if not all trees were killed. Practically all trees from larger stands were reported to have died. Until 1986 the situation worsened from year to year and from 1986 some of the younger trees within the decline areas which survived have shown first signs of recovery by forming new crowns above flat, senescent ones. The decline symptoms diminished significantly and unusual mortality stopped by late 1980s. This widespread fir dieback was explained as a complex/decline disease (Ciesla and Donaubauer, 1994) with very long drought periods and also probably frost as main inciting factors and various biotic factors (stem and root rot fungi) as predisposing or contributing factors (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994) . It was reported (Donaubauer, 1987) that younger trees were recovering after the stress period (1986 onwards) and that the climatic stress were shown by reduction of diameter growth in fir and other conifers in the region with few serious consequences on other conifers like Spruce, Bluepine, Larch etc. Considerable reductions in diameter growth had occurred in all tree species and the frequency which has increased since the late 1950s could be seen from the increment core samples taken and tested in the lab. Core samples were taken in various locations at different altitudes between 3,000 and 4,000 m from different conifer species. From the increment core samples results it was reported that most trees show evidence of severe growth depression since 1979 or 1980. Due to the specific physio-ecological conditions, the uppermost belt of fir weakened by over maturity and advanced decay was affected more seriously. Younger fir trees (80-120 years) with less decay were reported to show signs of recovery which was indicated by wider annual rings with some trees recovering from 1983 and other in the later years. The 1986 annual ring was reported to show maximum growth. It is reported (Donaubauer, 1986) that the primary cause of the decline in the late 1970s and early 80s is severe climatic stress (drought period), so therefore a climatic one due to the fact that growth depressions are present at same time in all conifer species (more or less serious). It was concluded (Donaubauer, 1994) that decline of fir stands in higher altitudes in Bhutan must have been primarily due to moisture conditions in general since they being more sensitive than stands at lower altitudes.

Moreover it is reported (Donaubauer, 1994) that data on meteorological parameters was lacking but local foresters reported on major perturbations observed during 1970s and early 1980s. The monsoon was reported to have ended several weeks earlier than usual and interrupted by two or three dry weeks sometimes and less fog observed in the fir belt.

The extent of the decline was not known exactly but estimated to range between 6,000 and 10,000 hectares (Donaubauer, 1994). It has long been known by ecologists and foresters that climatic stress has major influence on forest health (Allen *et al,* 2009). Climate influenced forest dieback awareness and interest is not new (Auclair, 1993; Ciesla and Donaubauer, 1994) since it is historically known that episodes of massive forest mortality are triggered by natural climatic variation (Swetnam and Betancourt, 1998). Several examples of climatic water and heat stress driven forest mortality since 1970 based on global review of more than 120 documented examples are reported (Allen *et al.,* 2009 in Allen, 2009).

Such droughts were reported to be observed at the same period in the Western Himalayas and Pakistan which was followed by severe bark beetle problems. Similar conclusions have been drawn in connection to forest declines of broadleaf species in the Western Pacific region where fog and clouds occur quite often and such stress factor occurred around the same time in a specific altitude.

‘‘Dieback at the stand level are death of groups of neighboring trees and the structural patterns of canopy breakdown’’ (Mueller-Dombios, 1991; Sakamoto *et al.,* 2003). Similarly a working hypothesis presented by Mueller-Dombios (1985) for the Ohi’a dieback in Hawaii stated that ‘‘dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of forest stand maturity’’.

Forest mortality usually involves many, interacting factors ranging from drought to insect pests and diseases which often make identification of a single cause impossible. However forest health problems is usually caused by abiotic stress factors with climate stresses as a primary triggering factor for many forest insect and disease outbreaks (Desprez-Loustau *et al.*, 2006; Raffa *et al.*, 2008). Some massive outbreaks of forest insects causing tree mortality is attributed to climatic factors (Raffa *et al.*, 2008) since population dynamics of forest insects and fungal pathogens is directly affected by climatic conditions (Hicke *et al.,* 2006). Forest dieback is often a non-linear process regardless of the exact mechanism which emerges abruptly at a regional scale when climatic conditions surpass tree species physiological thresholds of tolerance or trigger insect pests’ outbreaks (Allen, 2007). It is commonly reported near the geographic or altitudinal margins of a forest type or tree species (Jump, Hunt and Penuelas, 2006), generally near its historic thresholds of climatic suitability where the most sensitive response to climate fluctuations is expected. Drought related forest mortality has recently been documented from all wooded continents and from diverse climatic zones and forest types (Allen, 2009). Drought and heat stress induced by climate have potential to cause dieback across a wide range of woody vegetation types around the planet (Allen, 2009). In many parts of the planet, in relation to these changes climate related forest mortality is reportedly increasing. It is reported that although it cannot be concluded from the available evidence, yet it is possible that increasing reports of dieback represent just the start of globally significant increase in problems associated with forest health and dieback. Dieback problems are reported since 1970 under relatively modest 0.5 degree Celsius increase in the earths mean temperature and drying climate in some areas (Seager *et al.*, 2007).

2.2 Fir Forests of Bhutan

In Bhutan, the temperate conifer forests form the natural vegetation in mountainous places at elevations between 2,100 and 4,200masl. Conifer forests occupy about 24% of the total land area of the country and mainly consists of Eastern Himalayan Fir (*Abies densa*.Griff), Eastern Himalayan Spruce (*Picea spinulosa* Griff), Himalayan Hemlock (Tsuga dumosa) and Himalayan Bluepine (*Pinus wallichiana*) (Grierson-Long, 1983; Rosset, 1999). Other conifers and many broadleaved tree species *(Rhododendron spp., Acer spp., Betula spp., Sorbus spp., Populus spp. and Salix spp.*) are often found mixed with the previously mentioned main conifers or sometimes on particular sites dominate forest stands (Grierson-Long, 1983; Rosset, 1999 in Kirisits *et al.*, 2007).

The East Himalayan Fir (*Abies densa* Griff.) forests occupy 11% (3, 453 sq.km) of the area of Bhutan (LUPP 1995) and occur at altitudes between about 3,000 to 4,000masl (Donaubauer, 1994). They are intermixed in the lower ranges (drier areas) with transition to mixed conifer belt with Spruce (*Picea spinulosa), Picea brachitylla,* Larch (*Larix griffithiana),* Juniper *(Juniperus recurva) and* Bluepine *(Pinus wallichiana)*. In the higher ranges with high precipitation and fog environment, they are intermixed with some Larch (*Larix griffithiana*), Juniper (*Juniperus recurva*), Hemlock *(Tsuga dumosa),* Spruce

(*Picea spinulosa)* & *Picea brachitylla*, as well as broadleaf species like *Betula utilis*, several *Acer spp.,* several *Sorbus spp.,* and tree *Rhododendron spp***.** A typical monsoon climate is reported (Gratzer *et al.,* 1997) to prevail throughout its range with heavy precipitation from June to September with a rather dry spring and fall. During winter temperatures frequently fall below zero centigrade with some precipitation in the form of rain and snow. Snow cover on the ground usually does not persist very long because of strong solar radiation at above 3,000 m and about 28 degrees north latitude. Firs at their ecological optimum forms single tree species stands over large areas i.e. mono-specific which regenerate from single tree gaps formed by breakage of severely rotten trees (Gratzer *et al.,* 1997). In fir forests the under-storey vegetation is usually dominated by dense and old *Rhododendron species* (around 47 species recorded). For the natural fir regeneration the Rhododendron jungle is reported to be of immense importance since it serves as protection against browsing by cattle, yak and wild animals (Donaubauer, 1994).

For sustainable agriculture, firs provide important timber and non-timber forest products and are habitats of important flora and fauna. Commercially fir is used for making shingles and other local needs for furniture, construction wood etc. But other conifers especially Bluepine (*Pinus wallichiana* A.B.Jackson) are preferred for many purposes which is the reason fir forests were able to grow without major disturbances from major cuttings or any other commercial ventures. It is reported (Donaubauer, 1994) that the real age of older trees cannot be determined by annual ring analysis primarily due to heart rot diseases and the sound part is reportedly older than about 200-300 years.

"Strong local winds occur due to the large vertical differences in topography. Storms of sufficient strength to cause large to meso-scale wind-throw or windbreak are reported not to occur. Fog is common in summer and in winter making a moist environment for fir forests" (Gratzer *et al.,* 1997).

Bhutan has a forest cover of 72 percent (approx.) of its total land area and policies to keep at least 60 percent of its land area forested for all times is enshrined in the Constitution of Bhutan, 2005. The policy of the Royal Government of Bhutan is to manage part of the fir forest for commercial timber production, at the same time protecting in national parks and forest reserves (Gratzer *et al.,* 1997).

2.3 Tree Regeneration in Disturbed Sites

Disturbances (i.e. discrete events which disrupt ecosystems leading to a change in resources (White and Pickett, 1985) trigger subsequent regeneration processes in most forested ecosystems (Veblen, 1982). The various disturbances differ among each other in their effects on tree regeneration. Regeneration that is established prior to disturbance, so called 'advance tree regeneration' almost completely survives some disturbances like wind-throws or tree diebacks. In contrast, tree seedlings and saplings are often destroyed during normal tree harvest and salvage logging or during ground fire. Regeneration can be natural or artificial. Hubbard *et al,* 1998 define "natural regeneration" as 'young plants produced from natural seed fall or from stump or root sprouting in openings formed after existing plants are cut, burned or blown over' and "artificial regeneration" as 'planting or purposefully seeding trees in a previously harvested area'. The success of natural regeneration generally depends on survival and dispersal of seeds and seedlings. During the juvenile stages of seedlings high mortality occurs due to various factors like climatic, edaphic, biotic and genetic factors. Growth and mortality of seedlings are the most vital in determining the survivor of juvenile trees in natural regeneration as many trees die without reaching maturity (Messier *et al.*, 1999). Even after establishment, the greatest numbers of seedlings in several forest types die during the first summer (Greene, D.F 1999). Initial establishment stage is more sensitive to soil moisture availability than radiation (Oosting and Kramer, 1946). Successful seedling establishment and subsequent survival and growth sufficient to ensure recruitment are both required for successful tree regeneration (Thomas *et al.,* 1998). In regeneration processes, seedling establishment is an important limiting factor leading to future tree population's spatial distribution (Rey and Alcantra, 2000). Subsequent seedling survival is subject to an important natural selection (Clark and Clark, 1989). In long lived woody species temporal variability in recruitment success is very common (O'Connor, 1995; Duchesneau and Morin, 1999). In populations with generally low annual recruitment success, pulse regeneration dynamics can occur as in forests with dense under storey of monocarpic bamboos (Janzen, 1976; Yamamoto *et al.*, 1995; Taylor and Qin, 1998a, 1998b). In central Bhutan successful regeneration of *Abies densa* forests with bamboo (*Yushania microphylla*) under storey was not found to be dependent on resource pulses from synchronized die back of the bamboo (Gratzer *et al.*, 1999). In these forests presence of regeneration niches like nurse logs contributed to the survival of a higher proportion of seedlings. Favorable conditions are frequently associated with fluctuating climatic conditions (Villalba and Veblen, 1998) and fluctuations in competing populations. However, regeneration does not depend on plants alone as the process is influenced highly by physical factors (light, temperature, moisture, nutrients and disturbance regimes) and biotic factors (herbivory, disease and competition with plants and animals) (Barnes *et al.,* 1980, 1998). Other sources of variation such as changes in land management or change in herbivore populations may also be reflected in the temporal variation of regeneration success (Peterken and Tubbs, 1965). Over grazing, poor site conditions, changes in soil properties, presence of and competition with aggressive weed communities and herbivory are the commonly cited causes for failure of natural regeneration (Stanturf *et al.,* 1998, 2001).

2.3.1 Tree Regeneration and Micro-sites

A forest site is an area that requires homogenous silvicultural practice regarding species choice, management, amelioration and expected yields (Louw, 1995). Sites will be relatively homogenous regarding soils, climate, parent material and topography.
Disturbances can also cause favorable and unfavorable micro-sites for tree regeneration. In forest regeneration, micro-site under forest canopy and their conditions are important factors because they influence the establishment of seedlings of component tree species (Harper, 1977; Grubb, 1977; Duncan, 1991). Micro-sites are defined as 'the areas that differ in environmental characteristics on the spatial scale of an individual seed or seedling (Titus and Moral, 1998; in Wangchuk, 2007). When a micro-site is characterized by a set of environmental conditions that meet the demands of a given tree species for establishment and growth, this site is referred to as a 'favorable' micro-site (corresponding to a 'safe' site as defined by Harper *et al,* 1965). Inside gaps micro-site characteristics are completely different forming specialized micro-sites which can be the regeneration niche (Grubb, 1977) or a safe site (Harper, 1977) for germination of certain species. The forest floor provides regeneration habitats generally consisting of various

substrata such as mineral soil, litter, mosses, nurse logs etc., which may provide safe site for establishment depending on species and seed size (Sugita and Tani, 2001). Even within the same substratum micro scale environmental conditions vary due to the micro relief of the ground surface, soil depth, litter layer thickness and undergrowth coverage (Hisashi *et al.,* 2001 in Gyeltshen, 2008). Niche differentiation may allow for coexistence of tree species in forests since resulting differences in resources may support establishment of certain species depending on a differential response of the species to the micro-sites (Newman, 1982 in Sugita and Tani, 2001). Micro-site requirements in different species may differ and some species may coexist (Newman, 1982 in Sugita and Tani 2001). On most soil types natural regeneration can occur because the early establishment phase depends more on micro-site conditions of the germination substrate at the soil surface than the soil type itself (Robert, 1997). However seedling establishment after disturbance depends on a number of factors such as seed supply from mother trees, suitable substrate, seed predation and climatic variability (Coates, 2000; Le Page *et al.,* 2000).

Generally a thick layer of litter on forest floor inhibits roots of small seedlings from reaching the mineral soil (Knapp *et al.,* 1982; Gray *et al.,* 1997). Fir seedlings which germinate from large seeds with long roots gets established on soil or nurse logs (Taylor *et al.,* 1988) and similar results was observed in regeneration of *Abies densa* growing on nurse logs in bamboo (*Yushania microphylla*) undergrowth in central Bhutan (Gratzer *et al.,* 1999; 2002). Sugita *et al.,* (2001) observed that in non-ground sites seedling recruitment was primarily determined by undergrowth conditions; *Tsuga diversifolia* grow best on micro-sites with low bryophyte cover and *Abies mariesii* with high dwarf bamboo cover. Studies conducted by Harmon and Franklin, 1989 revealed that *Picea abies* seedling emergence was found high on moss species and similar result was shown with high *Abies densa* seedlings on moss mats in central Bhutan (Gratzer *et al.,* 2004a), but is not best for establishment of fir seedlings (Kjersti, 2002 in Tshering 2005).

Topography and micro-sites has a marked influence on plant communities (Peterson et al., 1990). Peterson *et al.,* 1990 observed huge variation between pits and mounds with the pit micro-sites having much greater species richness, total biomass and total tree stem density. According to Schönenberger (2002), rougher topography of a mountain forests have larger proportion of favorable micro-sites. Generally, micro-sites are more important on the sub-alpine than on the montane elevational level because of rougher clima. A characteristic for many high-altitude forests, a clumpy stand structure is a consequence of these favorable and unfavorable micro-sites (Brang, 1998).

However, tree regeneration is not only limited spatially by favorable micro-sites, but also temporally due to irregular seed availability. Seed production per tree is generally lower at higher altitudes compared to lowlands (Mayer and Ott, 1991; Mencuccini et al, 1995 in Kupferschmid *et al*, 2002) because years with high seed production (i.e. mast years = episodic, synchronized high seed production) become rarer **(**Mencuccini et al, 1995 in Kupferschmid *et al*, 2002). Recent forest ecology studies emphasize on the identification of possible environment or biological factors affecting seedling survival. Light environment is highlighted as one of the critical factors in forest habitats (Coates, 2002) and soil moisture can also limit recruitment success (Herrera *et al.,* 1994).

2.3.2 Tree Regeneration and Competition

Competition is a mutually negative interaction within and among species (Begon et al., 1996). Plants compete for resources and interfere in process of acquiring resources harming one another (Inderjit *et al.,* 2002) and through production of chemicals i.e. Allelopathy (Lambers *et al.,* 1998).

The competitive ability of an individual of one species reflects the extent to which survival and /or growth of another species is inhibited (Tilman, 1986; Morin, 1999). Dynamics and species distribution and evolution is possible to be influenced by this kind of phenomenon (Begon *et al.,* 1996). Among biological interactions, density dependent competition processes are observed in several seedling populations (Takada and Nakashizuka, 1996).

Since plants are not mobile like animals they are considered more susceptible since they cannot escape competition (Stilling, 1996). Four classification schemes based on which different types of competition namely; competition mechanisms, kind of competing entities, relative impacts of competitors upon one another and the resources that are basis of the interaction has been identified by Keddy (2001).

The under-storey competing vegetations influence on tree regeneration and establishment has driven research in the field of vegetation management to understand relations between trees and competitors (Pouliot *et al.,* 2006) and is well studied and documented (Gratzer *et al.,* 1999; Goreaud *et al.,* 2001; Balandier *et al.,* 2006; Pouliot *et al.,* 2006). Amongst understorey species, Rhododendron species (Gratzer *et al.,* 2004a) and Ericaceous plant species have shown to compete with and in some cases inhibit canopy tree regeneration (Nilsen *et al.,* 1999; and Nilsen *et al.,* 2001). The local species due to competition may be deprived of light and the affected species suffer from limiting light conditions affecting its growth eventually (Begon *et al.,* 1996). Several studies showed that shade tolerant native under-storey influence and contribute to complete failures in local canopy tree regeneration and recruitment; these include *Rhododendron species* (Gratzer *et al.,* 2004a; Beckage *et al.,* 2000; Baker and Van Lear, 1998), *Acer circinatum* (Wardman and Schmidt, 1998) and bamboos (*Chusquea spp*.: Veblen, 1982; *Sasa spp:* Yamamoto *et al.,* 1995; *Yushania microphylla*: Gratzer *et al.,* 1999). Bamboos form very dense undergrowth and compete for light strongly i.e. *Sasa kurilensis* with *Fagus crenata* (Nakashizuka, 1998), water and nutrients i.e. with *Betula ermanii* (Takahashi *et al.,* 2003). In Bhutan studies showed that dense *Yushania microphylla* bamboo growth lower light levels hampering survival of *Abies densa* seedlings and density decreased with increase in bamboo culm density (Gratzer *et al.,* 1999). Similarly *Rhododendron hodgsonii* understorey is reported to influence natural regeneration of *Abies densa* (Gratzer *et al.,* 2002; 2004a). The role of light in natural regeneration below canopy is complex since light promote both seedlings and its competitors (Hale, 2004). Competition may be controlled by removing the competitors from the area but stopping their migration back to the area may be a problem. Also removal of competitors may lead to unnaturally high growth of some species, the so called Cage Effect (Stilling, 1996). Robert (1997) observed that seedlings surviving the first season on weed free surface are often successful in competing with other vegetation while those germinating along with competing vegetation struggle to survive. Several studies showed high seedling and sapling recruitment after reduction of competitors by fire or logging (Gullison *et al.,* 1996; Fredericksen *et al.,* 2000; and Kennard, 2000 in Tshering 2005). Some studies in southern Appalachian forests showed that canopy openings enhance *Rhododendron* *maximum* thicket establishment (Clinton *et al.*, 1994; Woods ad Shanks, 1959; Beckage *et al.*, 2000 in Tshering 2005). Similarly successful regeneration and establishment of a variety of tree species was observed under Salmonberry (*Rubus spectabilis* Pursh), Salal (*Gaultheria shallon* Pursh) and *Kalmia spp* under-storey (Ducey *et al.*, 1996; Huffman *et al.*, 1993; and Tappeiner *et al.*, 1991).

Though it may be difficult to prove existence of competition through experiments, but the lack of it simply does not imply that it does not occur (Stilling, 1996).

2.3.3 Tree Regeneration and Forest Grazing

In Bhutan cattle grazing is a tradition practiced since times immemorial (Norbu, 2000) similar to many parts of the world where forest grazing is practiced (Bland *et al.*, 1994; Etienne, 1996; Roder *et al;* 2002b in Tshering 2005). Cattle grazing is integral part of the local farming systems and will continue to be so for a long time in agrarian community like Bhutan (Tenzin, 2008). The general view among foresters is the non- compatibility of cattle grazing and timber production (Gillet and Gallandat, 1996) and in Bhutan, foresters view it as a constraint on natural regeneration (Roder *et al.*, 2001).

The negative effects of grazing especially overgrazing (Frost *et al.*, 1986) on forests are many such as soil erosion, nutrient depletion, soil acidification, topsoil compaction, hydromorphic humus formation (Clary *et al.*, 1990; Glatzel, 1999), selective feeding habits which change vegetation and at times the entire plant community structure, breaking up ground cover, forest regeneration ,site quality (Barnes *et al.*, 1980, 1998 in Gyeltshen, 2008), trampling, defoliation, inhibiting seedling survival, altering shape of plant by repeated pruning (Crawley, 1986 in Gyeltshen 2008). One of the contributing factors affecting soil physical quality is soil compaction due to trampling (Imhoff *et al.*, 2000) that may affect movement of water and nutrient through soil (Di *et al.*, 2001). Trampling affects soil saturation capacity and root ratio (Gokbulak, 1998) and causes soil water infiltration reduction (Mwendera and Saleem, 1997). Due to runoff and soil erosion there may be increased losses of nitrogen (Wood *et al.*, 1989).

However positive effects of grazing are seed dispersal, providing regeneration niches through soil wounds and competition reduction when competitors are more palatable than tree species. In different parts of the world including Bhuan, studies show that moderate grazing reduces competition for tree species (Allen and Bartolome, 1989; Gratzer *et al.*, 1999; Norbu, 2000). If the grazing pressure is moderate, cattle do not browse conifer species especially *Abies densa* (Gratzer *et al.*, 1999) due to their high tannin contents (Hergert, 1989; Hernes *et al.,* 2000, 2004 in Tshering, 2005). All plant-animal interactions are not harmful as there are many mechanisms of mutualism involved (Krebs, 2001). Natural regeneration especially in conifer forests has been promoted by grazing (Gratzer *et al.*, 1999; Darabant *et al.*, 2007) and to promote regeneration can be used as a management tool by reducing competing undergrowth (Gratzer *et al.,* 1999; Norbu, 2000; Tenzin and Rinzin, 2003; Darabant *et al.*, 2007). At the same time growth of unpalatable shrubs and bushes may be favored as observed in Tsamdrog areas that were invaded by un-palatable shrubs and bushes (RGoB, 2001). In open areas cattle grazing limits the colonization probabilities of woody species (Crawley, 1983 and Seligman, 1996, in Tshering, 2005), and also documented as a hindrance for forest species seedling survival (Motta, 1996 and Pitt *et al.*, 1998 in Tshering 2005). Litter raking in forests cause soil acidification (Glatzel, 1999) and probable reduction in overall nutrient availability (McIntosh, 1997 in Tshering 2005). Grazed vegetation decreases in productivity (Vickery, 1981; and Belsky *et al.,* 1986 in Tshering 2005). In Bhutan studies showed that for maintaining agricultural production level, cattle grazing play a role in transferring nutrients from forests to the agricultural fields in the form of cow dung (Roder *et al.,* 2003). Nevertheless transferring high amounts of nutrients from forests causes severe nutrient depletion and soil acidification which in the long run will cause forest degradation and have negative impact on agriculture itself due to siltation and accumulation of debris in farmlands. Bhutanese farmers and herders have grazing rights (Tsamdrog) in some parts of forests set aside (F&NC Act, 1995, 2005) but grazing is not confined to Tsamdrog only (Norbu, 2000). In the policies of the RGoB, traditional rights are recognized whereby recent forest management plans and their objectives are geared towards promoting interaction between forestry and farming systems (FRDD, 2002). Since grazing involves exploitation of renewable natural resources, it is important to have a good knowledge on the process in maintaining ecosystem productivity (Wangchuk, 2002). The regeneration dilemma in conifer forests of Bhutan is the failure of natural regeneration in cleared areas incase *of Abies densa, Picea spinulosa and Tsuga dumosa* in western part of Bhutan which warrants special attention.

Photo 2: Browsed fir (*Abies densa)* seedling near a plot close to the herding footpath in the dieback affected fir forest on August 2008. (Source: Sonam Tobgay)

3 RESEARCH OBJECTIVES AND METHODS

3.1 Rationale

In the late 1970s and early 1980s, conifer forests in Western Bhutan were affected by widespread fir (*Abies densa* Griff.) dieback problems (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994). Fir dieback or decline is the most important health problem of fir forests in Bhutan (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994) where many fir stands over extensive areas were affected and at many places large portions if not all trees were killed. Practically all trees from larger stands were reported to have died. The decline was restricted to the upper elevations of fir zone and at lower elevations only on single trees or smaller groups the decline was observed. Moreover it is reported (Donaubauer, 1994) that data on meteorological parameters was lacking but local foresters reported on major perturbations observed during 1970s and early 1980s. The monsoon was reported to have ended several weeks earlier than usual and interrupted by two or three dry weeks sometimes and less fog observed in the fir belt. It was concluded (Donaubauer, 1994) that decline of fir stands in higher altitudes must have been primarily due to moisture conditions in general since they being more sensitive than stands at lower altitudes. Similar to the working hypothesis presented by Mueller-Dombios (1985) for the Ohi'a dieback which stated that ''dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of forest and maturity''. This widespread fir dieback was explained as a complex/decline disease (Ciesla and Donaubauer, 1994) with very long drought periods and also probably frost as main inciting factors and various biotic factors (stem and root rot fungi) as predisposing or contributing factors (Donaubauer 1986, 1987, 1994; Ciesla and Donaubauer, 1994) . The extent of the decline was not known exactly but estimated to range between 6,000 and 10,000 hectares (Donaubauer, 1994).

Mueller-Dombois, 1991 reported that dynamics of less diversity biomes is mainly influenced by the few canopy species dominating the vegetation cover. Gratzer *et al.,* 2002 reported that knowledge on fir forest dynamics is important for both sustainable management and nature conservation. Vegetation dynamics influencing factors act on different space and time scales (Spies and Turner 1999, White and Jentsch 2001 in Gratzer *et al.,* 2002). Multiple scale analysis of forest structure and regeneration will allow to identify the driving factors for forest dynamics particularly in areas where no information on the disturbance regime is available and information on autecological characteristics of trees is very less (Pabst and Spies, 1999 in Gratzer *et al.,* 2002). Stand structure is influenced by disturbance through modification of external environment (White & Pickett, 1985; Fujihara *et al.,* 2000).

Although several studies on conifer regeneration has been conducted in Bhutan, mostly in Central Bhutan. However it is reported (McKinnon 1995, Dhital, 1998 in Gratzer *et al.,* 2002) that the structure and dynamics of these forests are poorly understood and documented which poses problems for both sustainable forest management and nature conservation (Gratzer *et al.,* 2002). The fact remains that almost three decades after the massive dieback, there is lack of information on the regeneration and vegetation dynamics of the fir dieback affected stands in Western Bhutan since no study has been conducted till today. Forest regeneration and development begins from a disturbance (Yamamoto, 1992b; Runkle, 1998; in Nagaike, 2003).

Photo 3: The present condition of the dieback affected fir forest on the sub-alpine level in August, 2008. Open sites are presently occupied by *Juniperus recurva.*, *Salix spp.*, bushy *Rhododendron spp.*, *Berberis spp.* and *Rosa sericea* bushes. (Source:Sonam Tobgay)

It is the aim of this study which is a part of the larger ongoing conifer regeneration studies in Bhutan to address the following questions:

1. Is there regeneration in the massive dieback affected areas?
2. Is the area regenerating back with fir or it is being displaced by other conifer species and what is the present stand and regeneration population in the dieback stands?
3. How are different site factors like grazing, competing vegetation, micro-site, slope, topography etc. influencing regeneration if any?

3.2 Goals and Objectives

The general aim/objective of this research is to determine the regeneration status and dynamics of the dieback affected fir forests in Western Bhutan. The specific aim and objectives are:

i. To get quantitative data on tree regeneration in dieback affected *Abies densa* stands in Chamgang-Helela region (Thimphu), Western region of Bhutan.

ii. To develop hypotheses on factors influencing regeneration dynamics based on multivariate analysis of plot data.

iii. Provide information on how to manage fir dieback affected forests in the future.

3.3 Hypotheses

The study was based on the following hypotheses:

i. Fir is regenerating sufficiently in the die-back affected fir forest after the massive die-back in late 1970s and early 1980s leading ultimately to the same fir dominated mono-specific fir stands over time.

ii. Grazing by livestock, competing ground vegetation, micro-site, slope, topography are main factors influencing the regeneration process in the die-back affected fir forests.

4 STUDY AREA

4.1 Location

The study area falls in the Chamgang-Helela Forest Management Unit (CHFMU) which is located under the Thimphu Dzongkhag(district), in North Western Bhutan, between 89°20' and 89°30' East, and 27°17' and 27°28' North. The majority of the FMU occupies the Dagala Geog (block). The CHFMU is situated to the south east of Thimphu City in three valleys east of Simtokha. The ridge leading from Simtokha to the Talakha peak constitutes its western boundary, while the Longgey Zala ridge north of Kashim Derim Chu forms its northern boundary. The eastern and southern boundary is formed by the ridge between the FMU and the surrounding valleys. The access to the unit is through the northwest side of the FMU from Simtokha off the Thimphu - Phuentsholing road. Ground elevation in the FMU varies from approximately 2360 to 4100masl. The gross area is 4692.85 hectares.

4.2 Geology

The study area within FMU area is located in what is known as the Central Crystalline Zone of the Himalayas. It is dominated by metamorphic and granitic rocks, which are referred to as the Thimphu formation. The main rocks are gneisses. The main rock formations in the general area of the FMU are biotic schist, augen gneiss with quartz intrusions and occasional intrusions of granite. Generally, the soils have good permeability and moderate moisture retention. They are of medium texture and cation exchange capacity. They are moderately acid and are prone to further acidification.

4.3 Climate

The climate of the study area is typical for the Western part of Bhutan. The dominant climatic feature is the southwest monsoon in the period of June to September, during which most of the precipitation occurs. Precipitation changes greatly with altitude, with heavy monsoon showers common in the higher altitudes. Some years, heavy snowfall can occur in the winter months. High altitudes may offer severe winters and cool damp summers. The average monthly climatological data obtained from a meteorological station in Simtokha are presented in the following Figures 1 and 2**.**

4.4 Hydrology

The CHFMU within which the study area lies is in the watershed for the Thimphu Chu that lies within the sub-catchment of the Wang Chu. The Ola Rong Chu (which then feeds the Thimphu Chu) flows past the northern section of the FMU and is fed by the three tributaries that are totally encompassed by the FMU boundary. These tributaries are: Khasi Karim Chu, Badi Chu and Chamgang Chu. The settlers inside the CHFMU depend upon these streams and rivers for irrigating their cultivated lands and for drinking purposes. The nearby town of Babesa gets its drinking water directly from the Chamgang Chu. For this reason the upper portion of this Chu will be protected as per Forest Policy.

4.5 Topography

The FMU within which the study area lies extends from the bottom of the valley of Ola Rong Chu just above Simtokha and consists of three clearly defined valleys; Chamgang along the Chamgang Chu, Helela valley along the Badi Chu and the valley of the Khashi Kerim Chu. The altitude along the bottom of the valley is approximately 2400 meters whereas the altitude of the ridge that forms the FMU boundary varies from approximately 2800masl to 4100masl. There are areas of gently sloping land distributed throughout the FMU however the topography is mostly steep with gradients ranging from 50 to well over 100 percent. Toward the top of the ridges in the upper reaches of the valleys, the topography is very steep. This is particularly typical in the southern extremity of the Chamgang block.

4.6 Meteorological Stations

There are no meteorological stations within the Chamgang-Helela FMU. The nearest meteorological station is located in Simtokha.

4.6 Temperature

The monthly maximum and minimum temperature of the study area within the Chamgang-Helela FMU is given in the following graph.

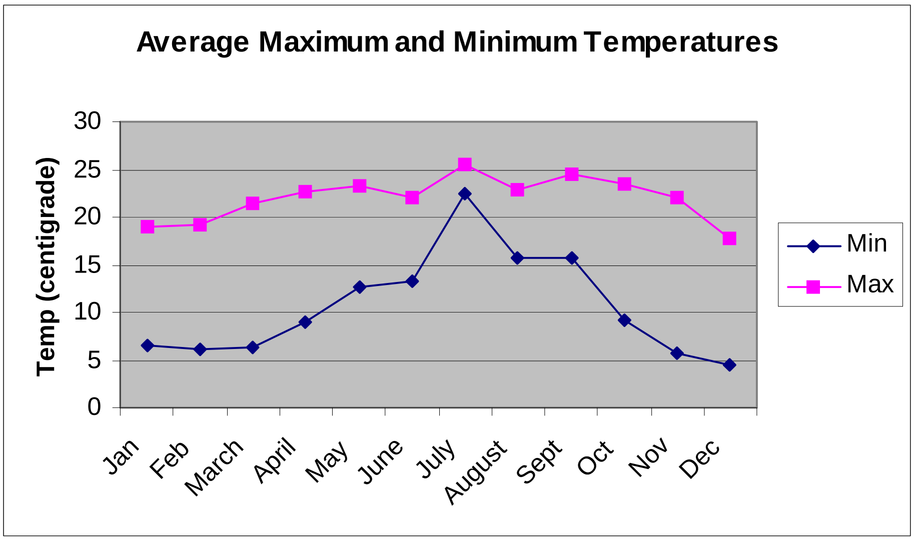


Figure 1 **(Source: FRDD)**

4.7 Precipitation

The precipitation of the study area within the Chamgang-Helela FMU is expressed in the following graph. Briefly during the winter months, the area can receive precipitation in the form of snow affecting mainly high elevation sites.

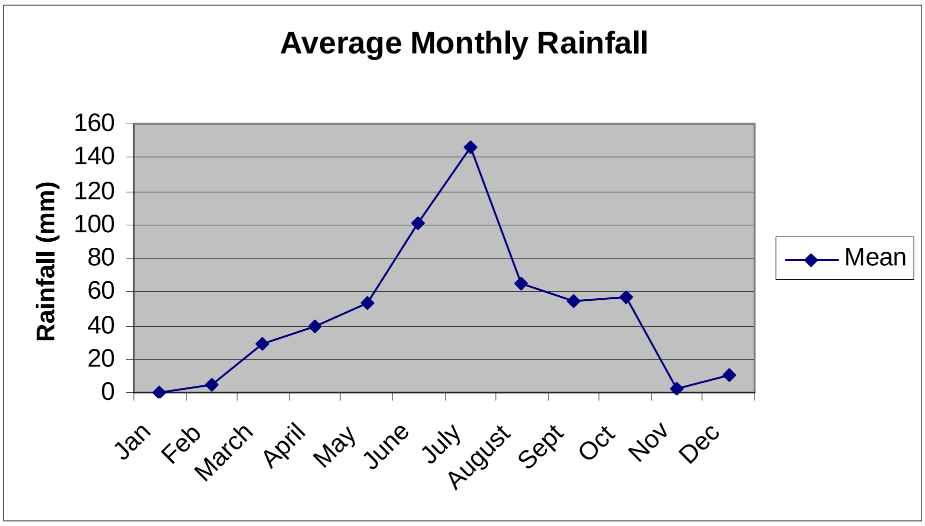


Figure 2 **(Source: FRDD)**

Although the above graph is representative of the average monthly rainfall, it is important to acknowledge that this data can vary drastically from the *minimum* to the *maximum* monthly rainfall. So much so that some months and years can be representative of drought.

4.8 Vegetation

No detailed classification of the vegetation in Bhutan has been undertaken. However, with minor variations, the classic work of Champion and Seth (1968) on the classification of forests in India, which included the Himalayas, could be applied to many of the forest types in Bhutan. Earlier treatments divided the country into three zones:

- A northern belt above 4,000masl, with no forest cover, only alpine ground shrubs and grasslands,
- A central belt between 2,000 and 4,000masl, containing the major temperate coniferous and broad-leaved forest types, and,
- A southern belt between 200 and 2,000masl elevation comprising sub-tropical vegetation.

On this basis, the study area within the Chamgang-Helela FMU falls almost entirely within the central belt.

4.8(a) Forest Type

Fir forest is characteristic of the highest forested ridges (3,200m) up to the tree line and occurs mostly as pure stands, except for a few hemlock and Birch. The dense canopy provides a humid environment for a luxuriant under-storey of Rhododendron and other shrubs. Nearer the tree line, the fir become stunted and is outnumbered by Juniper and Rhododendron. These higher elevation areas are where the fir dieback is occurring - and where the stands tends to become pure Rhododendron. Most of the fir at the higher elevations is over mature and shows a considerable degree of decay.

Table 1: Area Covered by Different Forest Types and Percentage of FMU Area

(Source: FRDD)

Forest Type	Area (ha)	Percent Area
Blue pine	955.71	20.36
Mixed Conifer	2 166.78	46.17
Hardwood	225.89	4.81
Fir	1 040.24	22.17
Total	**4388.62**	**93.52**

5 EXPERIMENTAL APPROACH

5.1 Field Work Data

The field work was done from mid-July to September, 2008, during the summer break of the academic term at BOKU. The research team from RNR-RC, Yusipang including staff of the National Herbarium and Botanical Garden, NBC was available to assist in the field throughout the data collection period.

The description of field data collection is discussed below:

Plot Layout:

A total of 20 temporary plots, each of 20x20 m size were randomly established in the study area, starting from the lower limit of the dieback zone. Plots were distributed randomly along both vertical and horizontal transects depending on accessibility, the plot to plot distance being kept at 50 m constantly whether vertical or horizontal.

Each plot was further divided into four quadrants (sub-plots); each of 10x10 m and all tree species and shrub species including saplings and seedlings, were recorded.

For tree regeneration within the quadrants, only the maximum and minimum height and age were recorded and the total numbers counted.

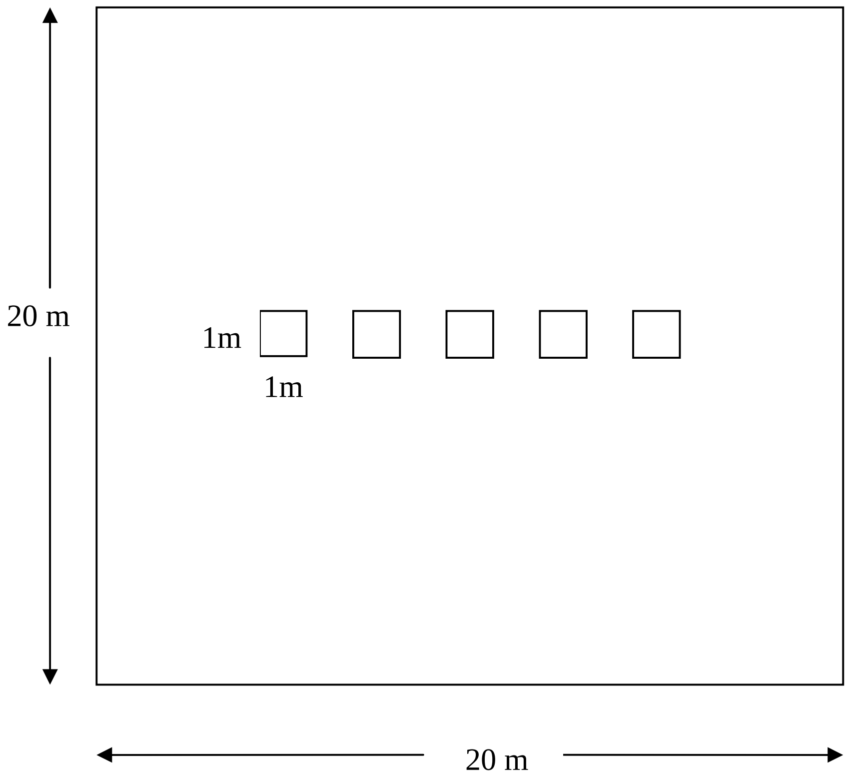
For tree saplings: height, number and DBH (diameter at breast height) if possible was recorded.

In the case of shrub species: height, number and cover percentage were recorded, and if possible DBH (diameter at breast height) too was recorded.

In the case of tree species: height, DBH (diameter at breast height), number and status (live or dead) were recorded.

Within each plot, 5 1x1 m mini-plots were selected systematically i.e. one at the centre of the plot and 2 mini-plots on either side in E-W direction with 1m distance between the mini-plots. Within each 1x1m mini-plots seedlings or regeneration below 1m height (species, height in cm, age in years, cover percentage) and herbaceous vegetation (species, cover percentage) was recorded.

With this procedure, a total of 100 mini-plots were described over the study area.



Design of Plot layout:

General Plot Characteristics:

General plot characteristics recorded included slope (%), aspect (degrees), altitude (masl), pH, moisture (%), shade (full, partial, open), micro-site (moss, mineral soil, organic matter, leaf litter and bog), and distance from migratory herding path. Grazing (impact of pastoral use) was assessed by indicators for trampling and browsing through hoof prints and browsing of shrubs and herbs.

Over-storey Tree Composition:

All trees within the sub-plot whether living, dead decaying and standing, dead decaying and downed was measured using diameter tape to the closest cm for DBH. A Spiegel Relaskop was used to measure the height of the trees to the closest cm. Species, height, DBH and status (live or dead) was recorded.

Under-storey Vegetation:

In each mini-plot of 1x1 m, the vegetation compositions was recorded by species, height and cover percentage for the herbaceous vegetation and species, height, cover percentage, number and age in case of the woody vegetation. Plants were carefully assessed for any signs of grazing damage.

Regeneration Assessment:

Regeneration was enumerated by species, height, age, cover and numbers and carefully inspected for signs of damage due to grazing.

Micro-site records included; mineral soil, moss, organic matter, leaf litter, and bog in cover percentage.

5.2 Data Analysis

Data were analyzed using Microsoft Excel (Office 2003) and SPSS (Statistical Package for Social Science) version 15.0 for Windows. Microsoft Excel was used for the initial data preparation and for the graphs. SPSS version 15.0 for Windows was used for univariate and multivariate analysis**.** The data was checked for outliers using box-plots and scatter-grams. Kolmogorov-Smirnov (KS) tests were used to test for normal distribution. Since most of the data were not normally distributed and could not be normalized by transformations, all statistical analyses were performed using non-parametric tests, unless otherwise reported.

To account for our observations of clustered fir seedlings, which indicate favourable combinations of site factors for the regeneration and establishment of fir, we decided to use a binary logistic regression analysis method to analyse the fir seedling probability in the mini-plots. This method allows one to predict the probability of a dependent variable (e.g. presence of a fir seedling) in dependency of different independent variables (e.g. site factors) (Brang *et al.* 2003; Knoke 2003a). This analysis, as a structure searching statistical method, calculates the likelihood of an occurrence of a fir seedling in the mini-plots (as the dependent variable) as affected by different independent variables (Backhaus *et al.* 2003; in Baier *et al.* 2005). This method is simple and robust and the SPSS version 15.0 for Windows provides numerous diagnostic opportunities. This analysis is not based on multivariate normally distributed independent variables and shares with metric and categorical variables (Backhaus *et al.* 2003; in Baier *et al.* 2005).

Therefore , the occurrence of, or the absence of fir seedlings in the mini-plots and the nominal scaled site variables were coded as shown in Table 2 below. As a result of dummy coding, the three nominal classes of independent variables were expressed by two new variables (Backhaus *et al.* 2003; in Baier *et al.* 2005). Interdependencies among the independent variables were tested by the existence of correlations using Spearman's correlation coefficients (2-tailed). Then ''stepwise forward'' option of SPSS was used to select and introduce only significant ($P < 0.05$) variables into the model. Negative parameters of the logit-function indicate decreasing probability of the occurrence of fir seedlings; while positive parameters indicate increasing probability of the occurrence of fir seedlings. Odd ratios were calculated to analyse the importance of the independent variable on the fir seedling probability (Backhaus *et al.* 2003; in Baier *et al.* 2005). Therefore, the increase or decrease (depending on the algebraic sign) of the independent variables by one unit increases or decreases the fir seedling probability by the odd ratio. The likelihood-ratio test, the Hosmer-Lemeshow test and the Nagelkerke R^2 were used as quality characteristics of the model (Backhaus *et al.* 2003; RRZN 2001; in Baier *et al.* 2005). For the quality of the model, the success of classification is important too. The classification was carried out on the basis of those observations which were used to estimate the parameters of the model. In order to assess the improvement of the model when additional variables were introduced, the reduction of the -2-log-likelihood-value (-2LL) was estimated (Knoke 2003a).

Photo 4: Plot falling in the open near a herding footpath which is occupied by *Juniperus recurva*, *Berberis asiatica* and *Rosa sericea* bushes and the ground cover occupied by herbaceous species like ferns, *Angelica spp*, *Fragaria nubicola* and *Potentilla spp.*

Table 2: Definition of classes of the variables used in binary logistic regression analysis

Variable Classes	Values in binary logistic regression
Dependent variables	
A fir seedling occurred in the mini-plot	1
A fir seedling did not occur in the mini-plot	0
Independent Variables:	
Ground coverage (herbaceous spp.)	Metric
Ground coverage (*Fragaria nubicola)*	Metric
Ground coverage (woody spp.)	Metric
Slope	Metric
Aspect	Metric
Distance of migratory herding path from mini-plot	Metric
Moss coverage	Metric
Live-trees present within 20	1
Live-trees not present within 20m	0
Mineral soil coverage	Metric
Organic matter coverage	Metric
Leaf litter coverage	Metric
Bamboo present within 1-2m	1
Bamboo not present within 1-2m	0
Shade category	Dummy variables
Open	0/0[a]
Partial shade	1/0
Full shade	0/1

[a] 0/0 acts as reference value for the two new dummy variables

6 RESULTS

6.1 Natural tree regeneration

i. The first objective of the study was to get quantitative data on tree regeneration in dieback affected *Abies densa* stands in Chamgang-Helela region (Thimphu), Western region of Bhutan. This was described based on the number of fir seedlings in the individual mini-plots of the overall study area.
Table 3 accounts for the 100 1m² mini-plots in systematic grids of the 20 plots in the study area (next page). The average density of fir seedlings was 6,000 ha^{-1} (Mean=0.6 and SD=1.3). The mean coverage of the ground vegetation over all the plots was high. Mini-plots with visible decayed fallen logs, decayed stumps and coarse woody debris were rarely found. The canopy gaps were characterised by different leaf litter types on the forest floor and therefore characterised by highly heterogeneous forest floor types. Bamboo and Ericaceous forest floor appeared on three sites.

6.2 Influence of site factors (variables) on the occurrence of fir seedlings in the mini-plots

ii. The second objective was to develop hypotheses on factors influencing regeneration dynamics based on multivariate analysis of plot data. For this independent variables of 26 mini-plots with fir seedlings were compared with 74 mini-plots without fir seedlings provided below in Table 4 which compares the independent variables of 26 mini-plots with fir seedlings and 74 mini-plots without fir seedling. The data are illustrated in Fig. 1.1, 1.2 & 1.3 which scored every row of Table 4 to 100% and therefore demonstrates the relative distribution of site factors in fir seedling mini-plots compared to mini-plots without fir seedlings.

Table 3: Number of fir seedlings per ha, variation in coverage of ground vegetation, occurrence of live fir trees within 20 m , distance from footpath and the micro-sites (moss, mineral soil, organic matter and leaf litter).

Plots	Fir seedlings (N/ha)	Mean coverage of ground vegetation (%)	Occurrence of micro-site types (% of occurrence in plots)				Distance from migratory herding path (m)
			Moss	Mineral soil	Leaf litter	Organic matter	
1	0	85.8	0	20	30	0	1
2	0	81.4	0	20	25	55	2
3	0	96.0	5	15	50	30	3
4	0	97.4	25	25	10	40	10
5	16,000.00	62.0	25	0	50	25	70
6	4,000.00	89.1	0	5	10	70	50
7	4,000.00	61.4	10	0	75	15	70
8	0	69.0	0	15	50	35	1
9	0	74.3	0	30	10	60	5
10	0	64.5	0	10	70	20	1
11	0	89.0	0	80	0	20	1
12	0	63.0	0	20	50	30	8
13	0	72.4	0	10	10	80	10
14	18,000.00	82.4	65	5	0	30	20
15	8,000.00	17.6	15	0	85	0	10
16	24,000.00	21.4	15	0	80	0	20
17	8,000.00	28.8	25	0	75	0	60
18	18,000.00	40.3	50	0	50	0	60
19	0	71.4	5	0	95	0	15
20	30,000.00	22.0	80	10	10	0	20
Mean value for all plots	6,500	64.5	16	13.25	41.75	25.5	21.65

Table 4: Occurrence of independent variables in mini-plots with fir and without fir

Independent Variables	Occurrence in mini-plots	
	With fir (n=26)	Without fir (n=74)
Micro -site (all mini-plots %)	100	100
Moss (%)	31.6	12.6
Mineral soil (%)	5.5	13.4
Leaf litter (%)	48.3	43.4
Organic matter (%)	15.5	32.1
Distance from existing migratory footpath (m) (mean/SD/SE)	39.23/24.1/4.7	15.47/21.65/2.51
Shade (all mini-plots- no/%)	100	100
Open	1/3.8	15/20.3
Partial Shade	16/61.5	34/45.9
Full Shade	9/34.6	25/33.8
Living trees within 10 m	23	47
Slope (Mean/SD/SE)	39.4/10.9/2.1	27.3/10.5/1.2
Coverage of ground vegetation (%) (mean)	44.1	71.6/23.6/3
Fragaria cover (%)	5.3	10.6
Herbaceous cover (%)	30.8	53.7
Woody cover (%)	8.2	7.2

n=number of mini-plots

n=26 for mini-plots with fir seedlings and n=74 for mini-plots without fir seedlings

As a result of clustering of the tree regeneration, there were only 26 mini-plots out of a total of 100 mini-plots with fir seedlings. The probability of finding fir seedlings in the study area was strongly influenced positively by the distance of the mini-plots from the migratory herding path, by the presence of moss cover and negatively less strongly by the altitude. Most fir seedlings were also found on micro-sites where the ground vegetation cover was not as dense as in plots without fir seedlings and in plots on steeper slopes (mean 39.4 %). In comparison the gentler slope (mean 27.3 %) surface plots were devoid of fir seedlings. Fir seedlings were present in mini-plots which are far from the path used by migratory herders. The presence of fir seedlings was linked positively to presence of live mature fir trees nearby. The presence of fir seedlings was also linked positively to the percentage of moss cover as forest floor cover. Altitude, organic matter and mineral soil were negatively correlated to the occurrence of fir seedlings in the mini-plots. Other site parameters like leaf litter and the presence of bamboo clumps showed no significant influence on the occurrence of fir seedling in the mini-plots. Site parameter like the amount of shade showed that in the open areas, fir regenerates poorly and in the case of partial and full shade, there is not much significant differences in fir regeneration between them. At the same time fir regeneration was comparatively better in partial and full shade mini-plots. However, statistically it was not significant in predicting the occurrence of fir seedlings.

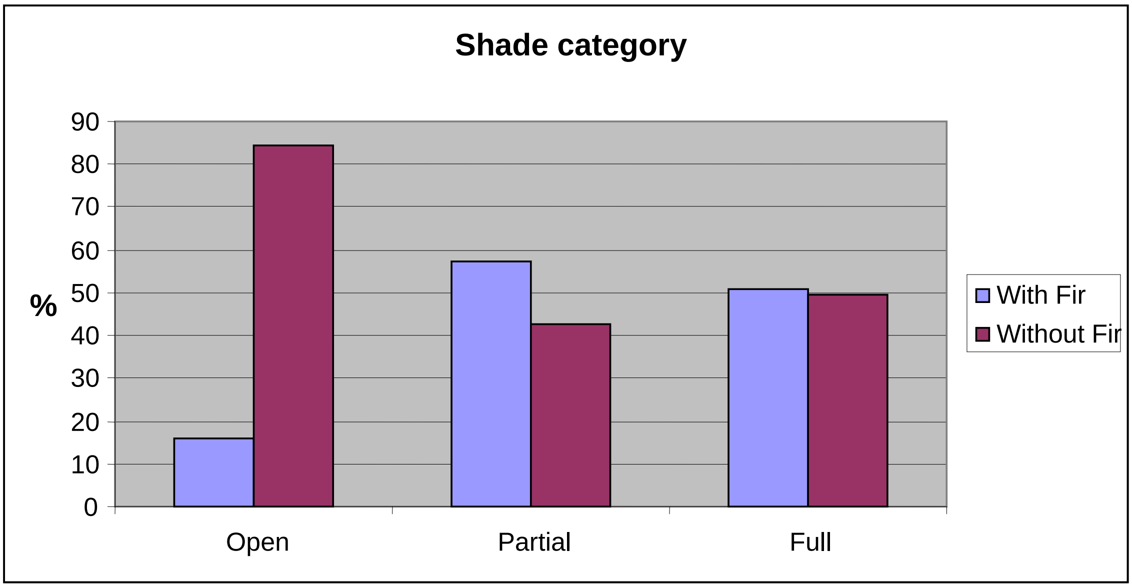


Figure 3.1 Percent rates of the total number (y-axis) within each class of independent variable (x-axis) in a comparison of mini-plots with fir with mini-plots without fir (each independent variable of Table 4 is set up to 100%)

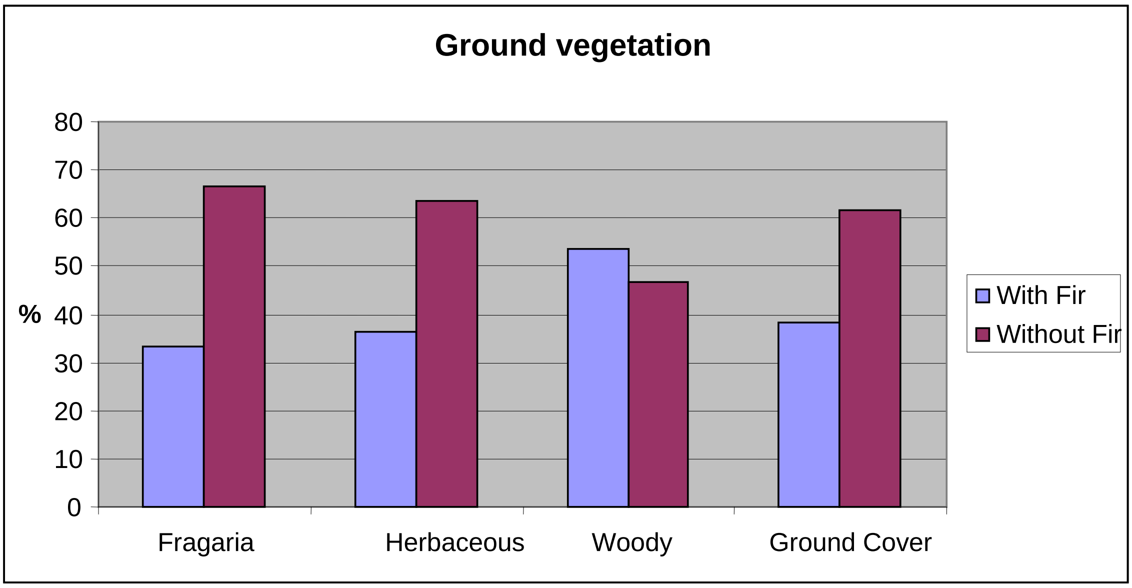


Figure 3.2: Percent rates of the total number (y-axis) within each class of independent variable (x-axis) in a comparison of mini-plots with fir with mini-plots without fir (each independent variable of Table 4 is set up to 100%)

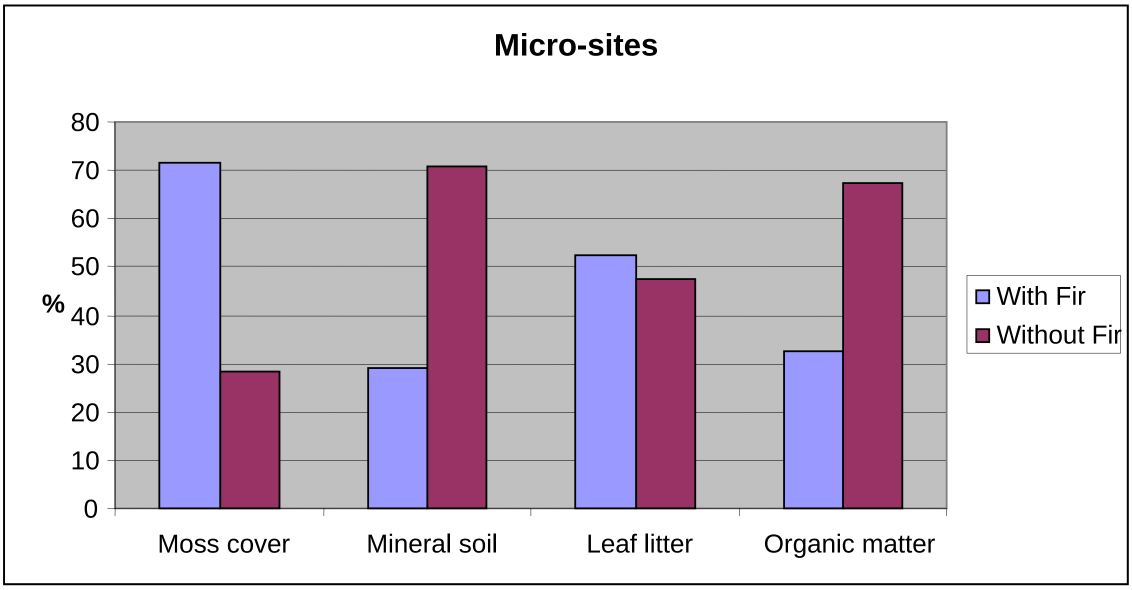


Figure 3.3: Percent rates of the total number (y-axis) within each class of independent variable (x-axis) in a comparison of mini-plots with fir with mini-plots without fir (each independent variable of Table 4 is set up to 100%)

Table 5: Spearman's rho correlation coefficient matrix of independent variables

		Fir Regeneration present
Live trees	Correlation Coefficient	.239*
	Sig. (2-tailed)	.017
Herding footpath distance	Correlation Coefficient	.526**
	Sig. (2-tailed)	.000
Moss cover	Correlation Coefficient	.494**
	Sig. (2-tailed)	.000
Slope	Correlation Coefficient	.425**
	Sig. (2-tailed)	.000
Ground cover	Correlation Coefficient	-.379**
	Sig. (2-tailed)	.000
Shade	Correlation Coefficient	.096
	Sig. (2-tailed)	.341
Bamboo	Correlation Coefficient	-.136
	Sig. (2-tailed)	.177
Aspect	Correlation Coefficient	-.057
	Sig. (2-tailed)	.570
Mineral soil	Correlation Coefficient	-.470**
	Sig. (2-tailed)	.000
Leaf litter	Correlation Coefficient	.183
	Sig. (2-tailed)	.069
Organic matter	Correlation Coefficient	-.368**
	Sig. (2-tailed)	.000
Altitude	Correlation Coefficient	-.239*
	Sig. (2-tailed)	.017
Fragaria spp. cover	Correlation Coefficient	-.070
	Sig. (2-tailed)	.490
Herb spp. cover	Correlation Coefficient	-.343**
	Sig. (2-tailed)	.000
Woody spp. cover	Correlation Coefficient	.285**
	Sig. (2-tailed)	.004

*.Correlation is significant at the 0.05 level (2-tailed).

**.Correlation is significant at the 0.01 level (2-tailed).

N=Number of cases=100

For the Spearman's correlation coefficient significance test, all independent variables were used. It showed high positive correlations ($P < 0.01$) with distance from the herding path, moss cover, slope and high negative correlations with ground cover, herb cover, mineral soil and organic matter. It also showed low positive correlations with live tree presence, woody seedling cover and low negative correlations with altitude. The results are given above in Table 5.

The basic statistical characteristics of the forward stepwise binary logistic regression analysis are given in Table 6. For the explanatory model too, all independent variables were used. With the binary logistic regression model including these predictor variables, 84 % of the cases were classified correctly, with 90.4 % correct classification for absence and 66.7 % for presence of fir seedlings. As a result of the non-significant ($P > 0.05$) influence on the probability of fir seedlings, the independent variables like ground coverage, shade, slope, live trees present, bamboos present, aspect, mineral soil, leaf litter and organic matter were excluded by the model. On the other hand, the P-values of the parameters of the three independent variables i.e. distance from the existing herding path, moss cover and altitude indicated that these variables included in the model were significant ($P < 0.05$). The slightly decreasing -2 Log Likelihood value following the introduction of a further variable in the model showed that fir seedling probabilities could not be predicted much better if further variables were included. The parameters distance from existing herding path, moss cover was positive, and so the fir seedling probability became greater as the distance from existing herding path and moss cover increased. In contrast, the parameter altitude is negative. Therefore, decreasing values of independent variable altitude led to an increasing probability of fir seedling occurrence. Because of low odd ratio, the independent variable altitude was of minor importance for the fir seedling occurrence probability compared to the distance from existing herding path and moss cover variables. The -2 Log likelihood-ratio-test value of 61.167 at $P = 0.011$ (should be smaller than 0.05, Chi-square value of 8.121 at $P=0.422$ (should be bigger than 0.05) of the Hosmer -Lemeshow test and the Nagelkerke R^2 value of 0.618 (value should be bigger than 0.2) indicated an adequate fit of the model to the data. With an accurate classification of 84 %, the performance and conformance of the model can be considered as well suited.

Table 6: Results of the binary logistic regression analysis for predicting the ''fir seedling'' probability (total data set n=100).

Model: Presence of fir seedlings

Variable	B	S.E	Wald	Degrees of freedom	p	Exp (B)
Distance from herding path	0.032	0.013	5.769	1	0.016	1.033
Moss Cover	0.074	0.016	20.557	1	0.000	1.076
Altitude	-0.025	0.009	8.329	1	0.004	0.975
Constant	76.237	27.225	7.841	1	0.005	1.3E+033

Quality characteristics of the model:

-2 Log likelihood test: $x^2 = 61.167$, $P < 0.05$

Hosmer-Lemeshow test: $x^2=8.121$, $P=0.422$; Nagelkerke $R^2=0.618$

Success of classification: 84 %

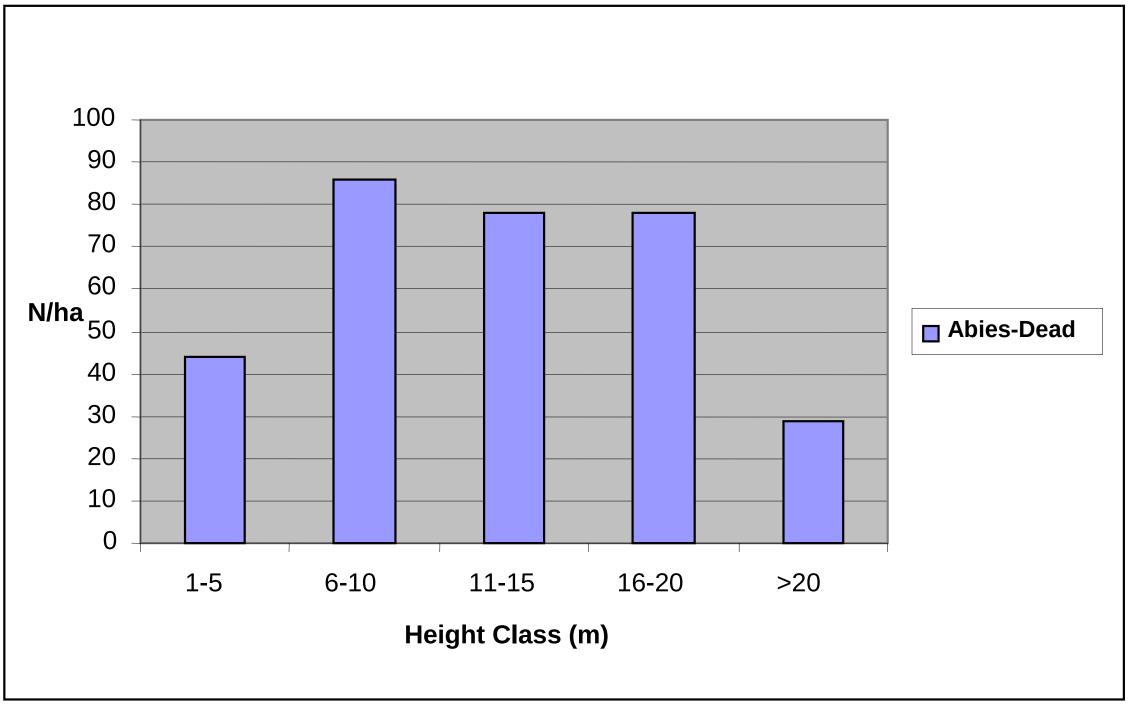


Figure 4.1: Height Class distribution of dead fir (trees) in the study area.

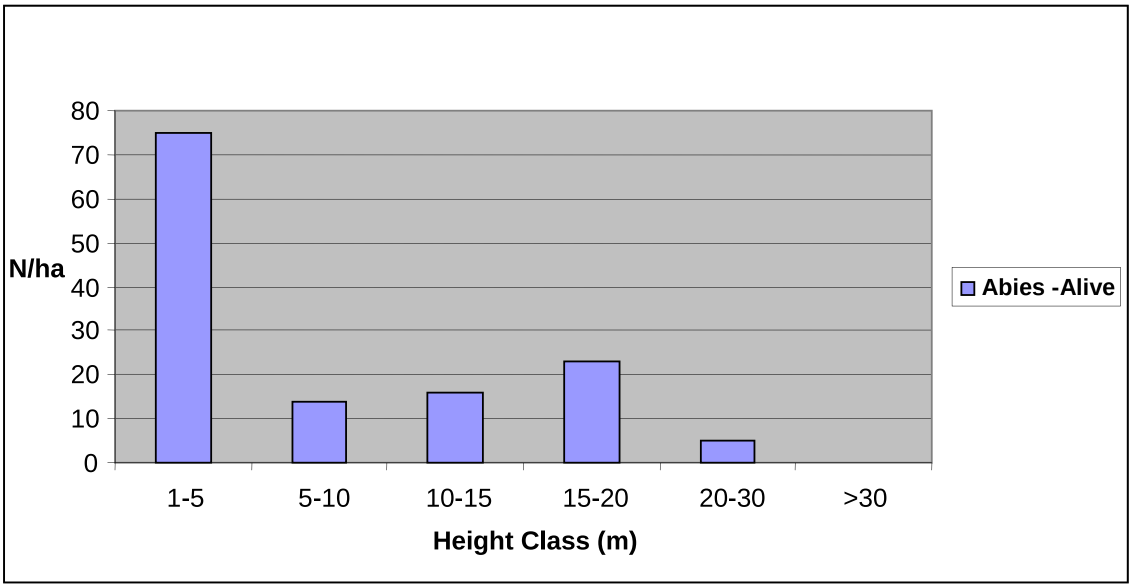


Figure 4.2: Height Class distribution of live fir (trees) in the study area.

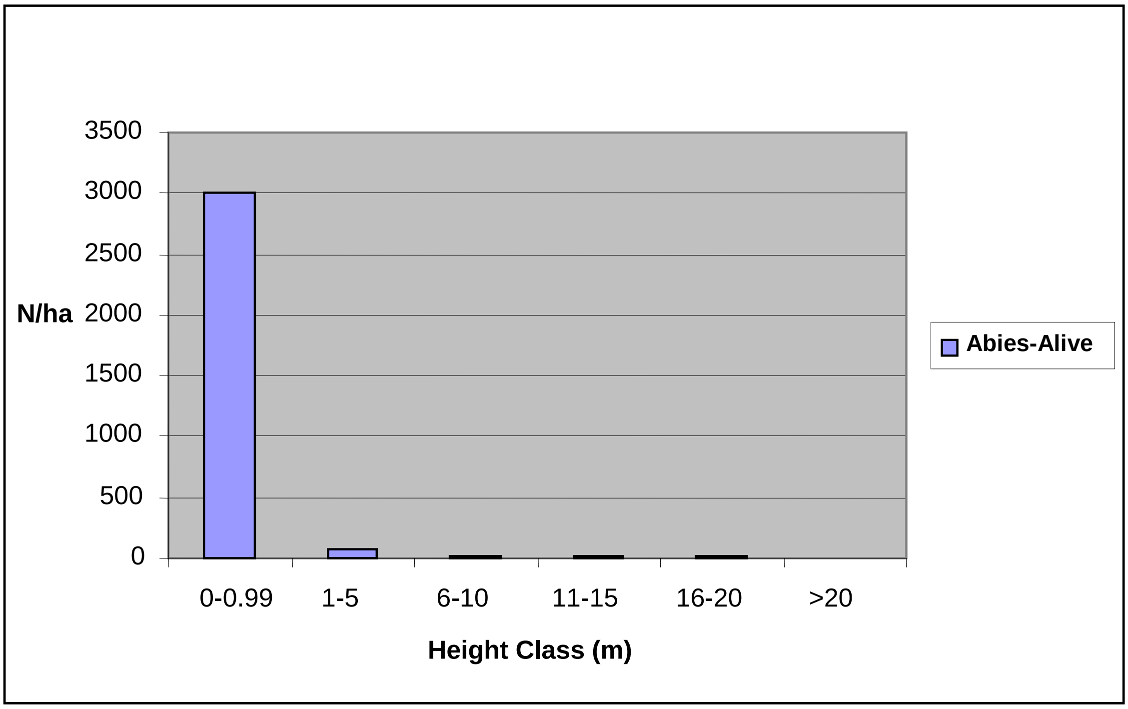


Figure 4.3: Height Class distribution of live (trees, seedlings and saplings) fir in the study area.

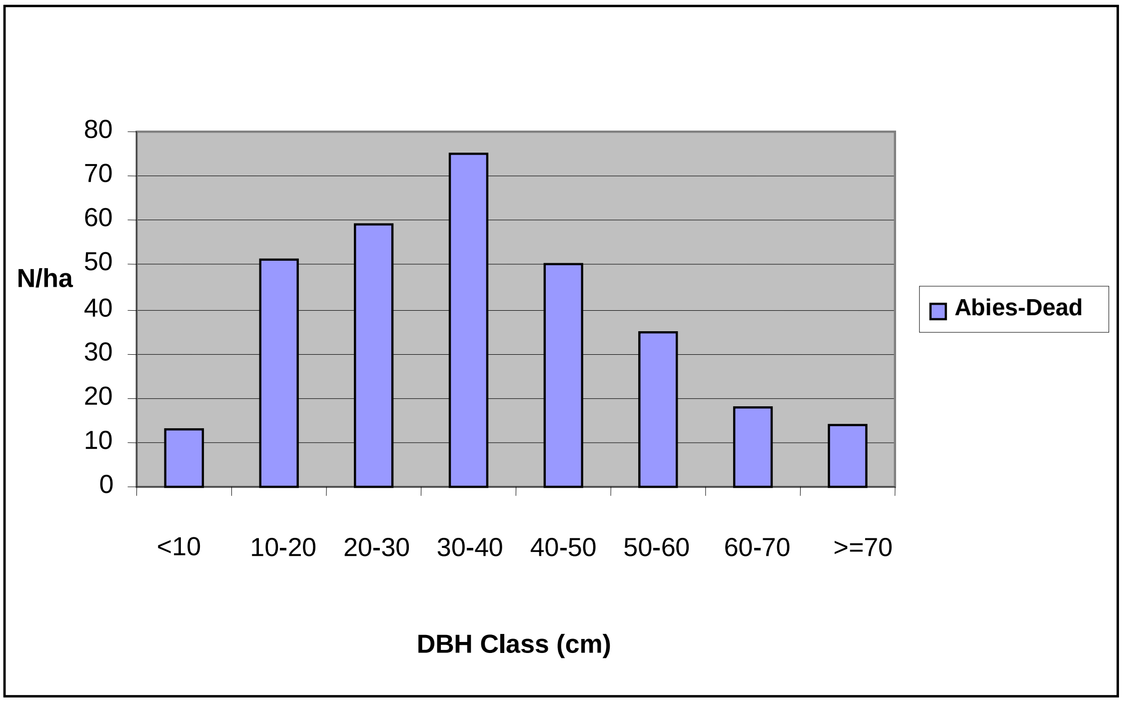


Figure 5.1: DBH Class Distribution of dead fir (trees) in the study area.

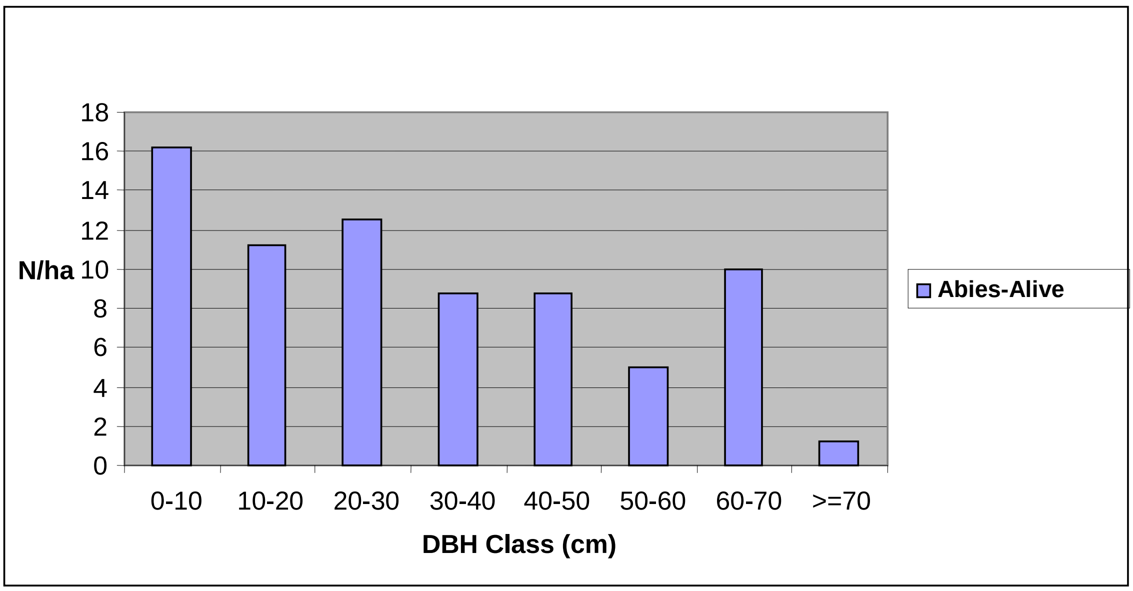


Figure 5.2: DBH Class Distribution live fir (trees) in the study area.

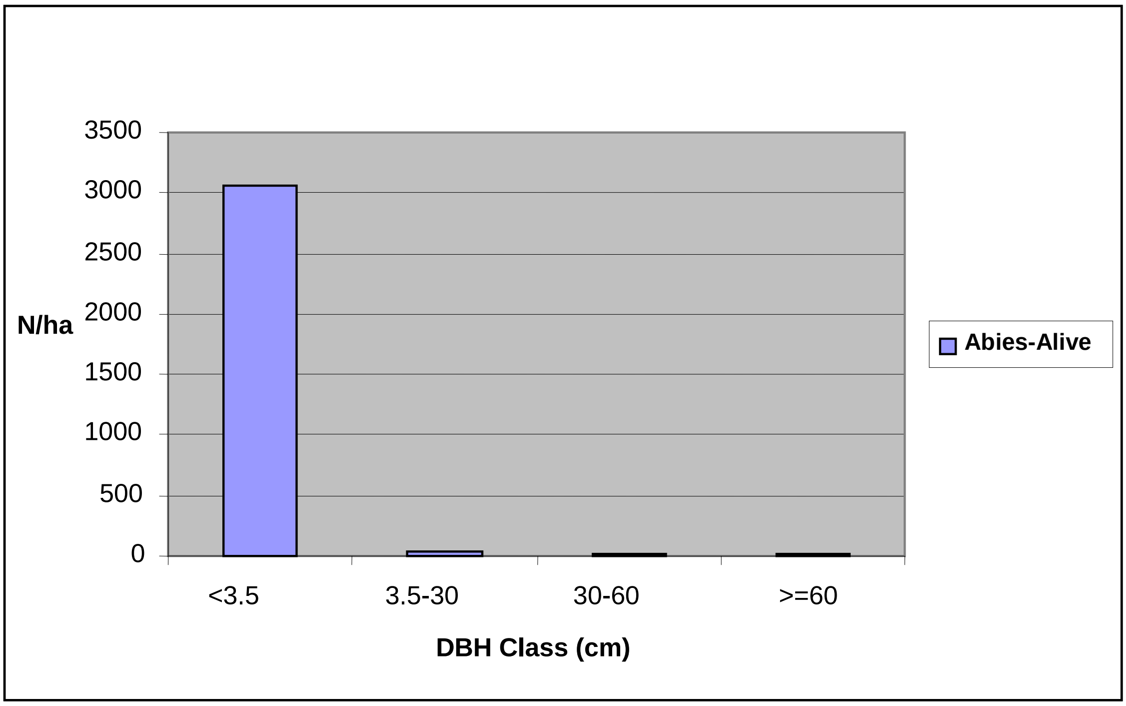


Figure 5.3: DBH Class Distribution of live fir (trees, seedlings and saplings) in the study area.

Figure 6: Density of fir seedlings (<1.3m) in the 20 plots of the study area.

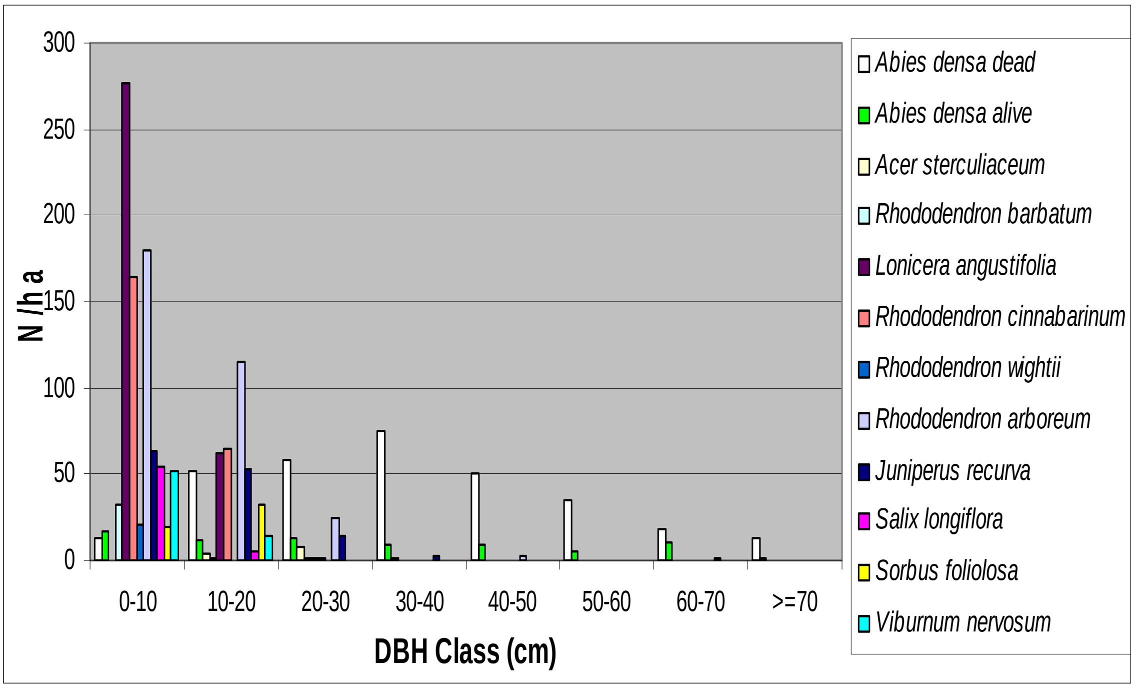


Figure 7: DBH Class distribution of live tree and shrub species in the study area.

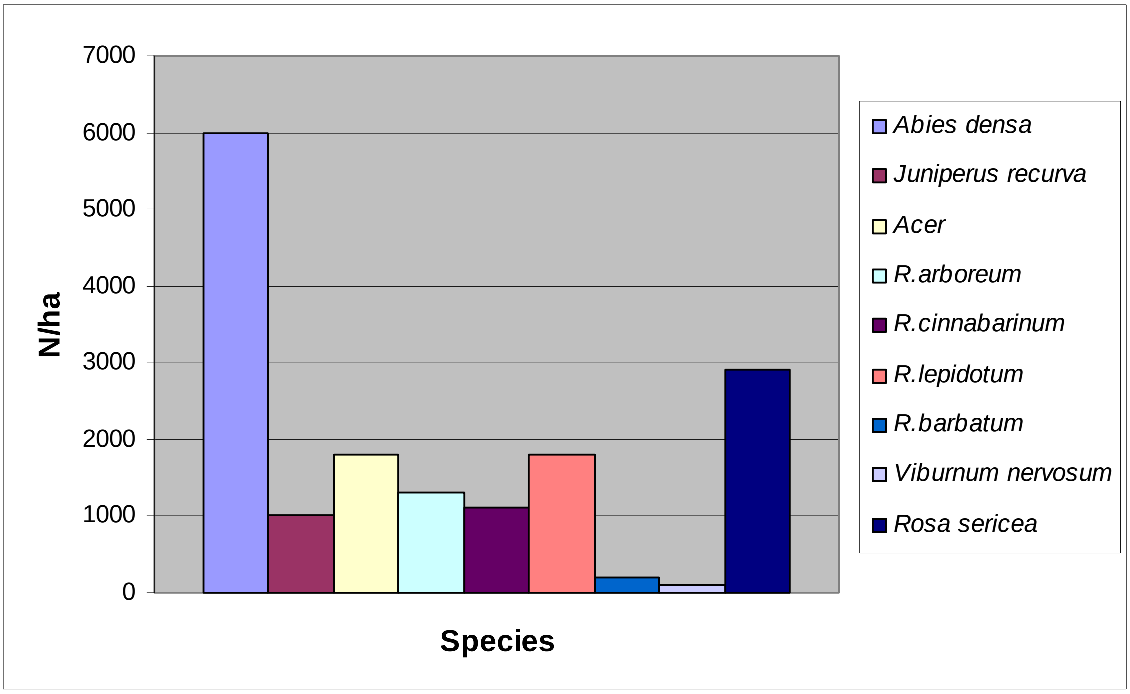


Figure 8: Density of seedlings (<1.3m) of different tree and shrub species in the 100 mini-plots of the study area.

7 DISCUSSIONS

7.1 Disturbance (Dieback) & Regeneration

Disturbances trigger regeneration processes in most forested ecosystems (Veblen, 1982), influence stand structure by modifying the external environment (White and Pickett, 1985), and thereby initiate ecosystem succession and dynamics (Gratzer *et al*. 2004). In our study site the dieback of the late 1970s and early 1980s caused 70% of the canopy trees to die. Only 30%, mostly sub-dominants and juveniles has survived. Disturbance events have strong and long-term impact on the structural diversity of natural forest ecosystems. The structural diversity determines the species diversity and resilience of forests. Biodiversity and resilience are generally higher in natural forests than in manmade forests (Jentsch, 2002; in Jentsch *et al*, 2007). The various disturbances are different in their effects on tree regeneration. Regeneration that is established before the occurrence of disturbance, so called 'advance tree regeneration' almost completely survives some disturbances like wind-throws or tree diebacks. In contrast, tree seedlings and saplings are often destroyed during normal tree harvest and salvage logging or during ground fire. Taller seedlings are more likely to reach the canopy when they are released by a disturbance (Marquis *et al*., 1992; in Fajvan *et al.*, 1996). After a disturbance, survivor trees compete for resources with members of the same cohort whether in similar or in different canopy strata. Younger cohorts maybe initiated by disturbance altering the stand age structure. Depending on spatial and temporal variations in disturbance induced mortality, older cohorts may suppress new cohorts or young cohorts eventually grow to compete in the same stratum (Oliver and Larson, 1996; in Fajvan *et al*., 1996). In the present study, it is obvious that the live trees in lower diameter and height classes must have been the advance tree regeneration which has survived the dieback of the previous mono-specific fir stands. At the same time the few mature live trees which are there have survived the dieback episode too and are presently serving as seed trees for the new regeneration of fir in these stands.

Concerning the deposition, germination and early establishment of a new generation of fir, the results in our study indicate temporal and in particular spatial variability. Several authors suppose that generally a thick layer of litter on forest floor inhibits roots of small seedlings from reaching the mineral soil (Knapp *et al*., 1982; Gray *et al*., 1997) making them prone to drying. Therefore a thick litter layer resulting from the needles shed by a large number of dying trees, could be detrimental to conifer seedling survival (Brang 1996, 1998; Greene *et al.* 1999; in Baier *et al.* 2005). This seems to be the case in the present study too. Even though fir seedling recruitment has taken place in the dieback affected stands, it is quite certain that fir regeneration did not take place for sometime after the dieback possibly because of the presence of large amounts of dead leaf and woody coarse litter on the forest floor which might have prevented seedling germination and establishment initially. However the possibility of adverse environmental conditions particularly dry moisture conditions, or fructification of weakened trees cannot be ruled out either.

This can be inferred from the 'reverse J' shape of the height and DBH class distribution graph of live fir which shows that fir seedling recruitment has not been continuous since the dieback. Nevertheless, replacement dieback recovery is likely to occur in the present study stands since dominance by under-storey species is unlikely due to the very low density of these species and also because of the fact that with the exception of Juniper, all the other tree and shrub species will most likely be shaded out once the fir trees grow up and form the canopy dominant trees. As fir is the most long-lived tree among the ones present in the study area, the number of firs will increase in closed stands over time while the number of other species will decline.

7.2 Development of the dieback stand

The type of plant community that will develop on a site after disturbance is governed by several factors including the species that were present on the site before the tree die-back, the distance away from seed sources, the seedbed and the weather conditions after tree death (Ross *et al.* 2001). Generally, the forest structure prior to disturbance plays an important role in influencing post-disturbance tree succession (e.g. Cooper-Ellis *et al.* 1999). After beetle-caused tree mortality there is often a release of co-dominant or under-storey trees (Holsten *et al.* 1995, Veblen 1991, Schulz 1996). Hogget (2000) found that maximum regeneration tends to be associated with maximum live canopy trees after a hemlock looper infestation in the interior cedar hemlock biogeoclimatic zone in Canada. Usually, absence of seed source near disturbed sites has been attributed in the literature to causing low levels of tree regeneration after disturbances (Lässig *et al.* 1995, Timoney and Peterson 1996).

The initial lack of regeneration as discussed above can be partially compensated for if new trees rapidly establish. Extrapolating from the numbers found in the permanent mini-plots, around 6,000 *Abies densa* seedlings per ha germinated and survived so far on the study site. Therefore, this small number of living *Abies densa* trees might restrict rapid forest recovery in the dieback fir forest in future, even though at present snags are collapsing and the decomposing logs should constitute additional niches (Grubb 1977) for new tree regeneration (Mai 1998, Stöckli 1995, Stöckli 1997, in Ulanova 2000a).

Our findings support the concept that retaining surviving trees (green tree retention) in disturbed sites and clear-cuttings is important for tree regeneration (Leder and Krumnacker 1998, in Beach and Halpern 2001). This can be confirmed with a significant Spearman's correlation ($P < 0.05$) between the presence of fir seedlings and presence of live trees i.e. a higher probability of finding fir seedlings in plots nearby the vicinity of live mature fir trees.

Several studies showed that rapidly growing species such as *Betula spp*. and *Populus spp*. established at severely disturbed sites, brushwood such as *Rubus spp.* dominated some sites after a disturbance only for 5-10 years (Whitney 1982; Ricard and Messier 1996, in Ulanova 2000b). Closed pioneer-crop stands of *Sorbus spp., Salix spp.,* or *Betula spp*. are only expected where the advance regeneration of such pioneer tree species is abundant or where large vegetation-free gaps are frequent (Schmidt-Schütz 1999; in Kupferschmid *et al.,* 2002). Neither was the case at our study site since pioneer species were encountered in few pockets only and were not abundant nor were very large free gaps common. Therefore, we assume that a pioneer tree stand will most likely not develop in the present study area. For this reason, light demanding species like *Juniperus recurva*, *Lyonia ovalifolia*, *Rosa sericea, Lonicera angustifolia* and *Rhododendron lepidotum* which are frequently encountered in open sites will probably be present in the dieback affected stands only until the *Abies densa* trees have grown so much that they provide too much shade and then they will disappear.

As was hypothesized for our study area, we conclude that fir is regenerating sufficiently in the die-back affected fir forest after the massive die-back in late 1970s and early 1980s leading ultimately to the same fir dominated mono-specific fir stands over time i.e. replacement dieback recovery (Mueller-Dombois 1991, and Sakamoto *et al*. 2003). The average density of fir seedlings for the entire area is 6,000 ha^{-1} which in comparison to seedlings of other tree and shrub species (Fig 8) is by far the highest of all trees in the study area. However, the stands will be patchy, with a mosaic of dense and widely spaced fir seedlings since almost half of the study area is devoid of fir regeneration (Fig 6).

7.3 Factors influencing fir regeneration:

Factors commonly attributed to failure of natural regeneration are over-grazing, poor site conditions, changes in soil properties, presence of and competition with aggressive weed communities and herbivory (Stanturf *et al.,* 1998, 2001). In forest regeneration, micro-sites and their conditions are important factors because they influence the establishment of seedlings of component tree species (Harper, 1977; Grubb, 1977; Duncan, 1991).
When a micro-site is characterized by a set of environmental conditions that meet the demands of a given tree species for establishment and growth, this site is referred to as a 'favorable' micro-site (corresponding to a Harper's 'safe' site (1965). Inside gaps micro-site characteristics are completely different forming specialized micro-sites which can be the regeneration niche (Grubb, 1977) or a safe site (Harper, 1977) for germination of certain species. The forest floor provides regeneration habitats generally consisting of various substrata such as mineral soil, litter, mosses, nurse logs etc., which may provide safe site for establishment depending on species and seed size (Sugita and Tani, 2001). Even within the same substratum micro-scale environmental conditions vary due to the micro relief of the ground surface, soil depth, litter layer thickness and undergrowth coverage (Hisashi *et al.,* 2001 in Gyeltshen, 2008). Micro-site requirements may differ in different species and some species may coexist (Newman, 1982; in Sugita and Tani 2001). On most soil types natural regeneration can occur because the early establishment phase depends more on micro-site conditions of the germination substrate at the soil surface than the soil type itself (Robert, 1997). However seedling establishment after

disturbance depends on a number of factors such as seed supply from mother trees, suitable substrate, seed predation and climatic variability (Coates, 2000; Le Page *et al.*, 2000).

Disturbances can also cause favorable and unfavorable micro-sites for tree regeneration. Generally, micro-sites are more crucial in the sub-alpine than in the montane elevation level because of a rougher climate. A clumpy stand structure which is characteristic for many high-altitude forests is a consequence of these favorable and unfavorable micro-sites (Brang, 1998; Baier *et al.*, 2005). Similarly to the above findings, the results of the present study indicate that the site has both favorable and unfavorable micro-sites because of which the regeneration is patchy with a mosaic of densely and widely spaced seedlings in some sites and other sites completely devoid of regeneration (Fig). At the same time the distance of the mini-plots from the seed trees strongly influenced the fir seedling presence.

The data presented above in Table 4, and Figures 3.1, 3.2 & 3.3 indicated that the spatial distribution of fir seedlings establishment was not random and varies among different micro-site types. Similar patterns have been found in other studies (Brang 1998; Brang *et al.* 2003; Baier *et al*. 2005). The binary logistic regression analysis proved that different site factors significantly determine Grubb's regeneration niches or Harper's safe site for fir seedlings (Table 6). These micro-site types may have characteristics that promote seedling establishment while others inhibit the fir seedling establishment and occurrence.

However in the explanatory model, most independent variables for ground coverage, shade, slope, live trees present, bamboo undergrowth, aspect, mineral soil, leaf litter and organic matter were not significant and were excluded by the model for predicting 66.7 % probability of occurrence of fir seedling.

7.3.1 Micro-sites

7.3.1.1 Moss

Various authors supposed that fir regeneration is promoted by moss**.** Studies conducted by Harmon and Franklin, 1989 revealed that *Picea abies* seedling emergence was found high on moss species and similar results was shown with high *Abies densa* seedlings on moss mats in central Bhutan (Gratzer *et al.*,2004a). In the sub-alpine forests of Japan, conifer regeneration was reported to be fast on moss dominated forest floor (Nakamura 1990). It has been reported that for many tree species, moss patches provide an excellent seed bed by protecting from desiccation (Fowells 1965). On the contrary it is reported not to be best for establishment of fir seedlings (Kjersti, 2002 in Tshering 2005). However, it is documented that moss favors conifer seedlings survival depending on the structure of moss and seeds/seedling characteristics. The preference of fir for mineral soil and moss for its survival is also reported (Gratzer *et al.*, 2002). These findings align with our results that moss provided the best substrate for the recruitment of fir regeneration. Moss was consequently the most common substrate where fir germination was present (Table 6 & Figure 3.3).

Among the various substrates available for establishment and survival of fir seedlings in the sub-alpine forests of western Bhutan, bryophytes (20.8% of total study area) provided the most suitable substrate for fir seedling germination and establishment in this study.

7.3.1.2 Mineral soil

Disturbances such as tree fall results in bare soil in forests. For seedling emergence, micro-sites like bare mineral soil in forests are at times found suitable (Peterson *et al.* 1990; Baier *et al.* 2005). Contrary to that, in the present study bare mineral soil which was present in 13.3% of the study area was found to be negatively correlated to fir seedling availability which could possibly be due to dryness in the mineral soil in the absence of intact canopy cover due to large gaps in the crown cover and moreover since most of the plots where fir was absent was on open and upper ridges of the study area. Another possible reason could be due to soil compaction observed in those mini-plots falling near the migratory herding path due to cattle and human movement. This is evident from the high positive significant correlation between mineral soil and distance from the migratory herding path meaning that exposed mineral soils were generally encountered in mini-plots falling nearby the herding footpath.

7.3.1.3 Organic matter

Organic matter (27.6% of study area) which showed high negative significance with occurrence of fir seedling mainly because thick and un-decomposed organic matter was found in most of the mini-plots it occurred, thereby hindering seedling establishment.

7.3.1.4 Bamboo litter

Ground habitat conditions are dark (Oshima 1961) and dessicated (Hibino *et al.* 1981) where dwarf bamboo liter accumulates. In the present study, no fir seedlings were present on bamboo litter. Therefore, the lack of seedling survival on bamboo litter is probably due to dry conditions. In addition, the litter prevents the roots from penetrating into the moist soil.

7.3.1.5 Leaf litter

Presence of thick litter on the forest floor due to accumulation of fallen needles and dead coarse woody debris after the dieback may possibly be the reason for the lack of regeneration initially after dieback on the study site. Leaf litter (37.6 % of study area) did not have significant influence on the probability of occurrence of fir seedlings since in some mini-plots it promoted fir seedling regeneration while on the others it hindered fir regeneration. The variation in thickness of the leaf litter in different mini-plots can be attributed to this non-significant correlation. This maybe in conformity to the findings that generally a thick layer of leaf litter on forest floor inhibits roots of small seedlings from reaching the mineral soil (Knapp *et al.,* 1982; Gray *et al.,* 1997) and making them prone to drying, therefore detrimental to conifer seedling survival (Brang 1998; Greene 1999).

7.3.1.6 Shade

Amongst under-storey species, Rhododendron species (Gratzer *et al.,* 2004a) and Ericaceous plant species have shown to compete with and in some cases inhibit canopy tree regeneration (Nilsen *et al.,* 1999; and Nilsen *et al.,* 2001). The local species due to competition may be deprived of light and the affected species suffer from limiting light conditions affecting its growth eventually (Begon *et al.,* 1996). Several studies showed that shade tolerant native under-storey influence and contribute to complete failures in local canopy tree regeneration and recruitment; these include *Rhododendron species* (Gratzer *et al.,* 2004a; Beckage *et al.*, 2000; Baker and Van Lear, 1998), *Acer circinatum* (Wardman and Schmidt, 1998) and bamboos (*Chusquea spp*: Veblen, 1982; *Sasa spp:* Yamamoto *et al.,* 1995; *Yushania microphylla*: Gratzer *et al.,* 1999). Bamboos form very dense undergrowth and compete for light strongly i.e. *Sasa kurilensis* with *Fagus crenata* (Nakashizuka, 1998), water and nutrients i.e. with *Betula ermanii* (Takahashi *et al.,* 2003). In Bhutan studies showed that dense *Yushania microphylla* bamboo growth lower light levels hampering survival of *Abies densa* seedlings and density decreased with increase in bamboo culm density (Gratzer *et al.,* 1999). Similarly *Rhododendron hodgsonii* under-storey is reported to influence natural regeneration of *Abies densa* (Gratzer *et al.,* 2002; 2004a). The role of light in natural regeneration below canopy is complex since light promote both seedlings and its competitors (Hale, 2004). Competition may be controlled by removing the competitors from the area but stopping their migration back to the area may be a problem. Also removal of competitors may lead to unnaturally high growth of some species, the so called Cage Effect (Stilling, 1996). Recent forest ecology studies emphasize on the identification of possible environment or biological factors affecting seedling survival. Light environment is highlighted as one of the critical factors in forest habitats (Coates, 2002) and soil moisture can also limit recruitment success (Herrera *et al.,* 1994).

Differences in regeneration pattern with and without *Rhododendron hodgsonii* and bamboo (*Yushania microphylla*) under-storey and canopy layers explaining 90% variation of fir seedling occurrence is also demonstrated and reported (Gratzer *et al.,* 2002). Bamboo (*Yushania microphylla*) under-storey favouring continuous fir regeneration through fine scale breakage of branches providing enough light conditions for growth and survival is also reported. Similar to these findings, in the present study, amount of shade showed that in the open areas, fir regenerates poorly, while partial and full shade conditions of undergrowth seemed to favour fir seedling establishment with not so much significant differences in fir regeneration between them. However, statistically it was not significant in predicting the occurrence of fir seedlings.

7.3.2 Bamboo

Regeneration patterns related to microhabitat may differ depending on different undergrowth conditions (Sugita *et al.,* 2001). Several studies conducted in central Bhutan showed that successful regeneration of *Abies densa* forests with bamboo (*Yushania microphylla*) under storey was not found to be dependent on resource pulses from synchronized die back of the bamboo (Gratzer *et al.*, 1999). In these forests presence of regeneration niches like nurse logs contributed to the survival of a higher proportion of seedlings. Fir seedlings which germinate from large seeds with long roots gets established on soil or nurse logs (Taylor *et al.*, 1988a) and similar results was observed in regeneration of *Abies densa* growing on nurse logs in bamboo (*Yushania microphylla*) undergrowth in central Bhutan (Gratzer *et al.,* 1999; 2002**).** A similar result was observed by Nakamura (1992) in a moss covered forest floor on Mt. Fuji where *A. veitchii* seedlings was not dependent on peculiar substrata. Regeneration on sites with bamboo under-storey is also highly gap dependent but needs either destroying of the bamboo or the die-back of the under-story species after flowering (Gratzer *et al.,* 1997). In the present study, establishing such a relationship was difficult since bamboo undergrowth occurred in only 10 out of the total 100 mini-plots. However, no regeneration was observed in mini-plots of the present study falling under thick bamboo undergrowth with limited light and resulted in the presence of thick bamboo litter found in the mini-plots.

7.3.3 Ground Vegetation Cover

Competition is a mutually negative interaction within and among species (Begon *et al.,* 1996). Other micro-site types may inhibit successful seedling germination and sapling establishment. Competition of ground vegetation increases under oceanic climate conditions (Ott *et al.* 1997 in Baier *et al.* 2005). Robert (1997) observed that seedlings surviving the first season on weed free surface are often successful in competing with other vegetation while those germinating along with competing vegetation struggle to survive.

The competitive ability of an individual of one species reflects the extent to which survival and /or growth of another species is inhibited (Tilman, 1986; Morin, 1999). Dynamics and species distribution and evolution is possible to be influenced by this kind of phenomenon (Begon *et al.*, 1996). Among biological interactions, density dependent competition processes are observed in several seedling populations (Takada and Nakashizuka, 1996).

In conformity to the above findings, in the present study, fir seedling germination and establishment decreased on mini-plots with dense herbaceous ground vegetation. However it is difficult to ascertain the original seedbed during seed germination, especially if ground vegetation hindered the early establishment of fir, or if fir reduced ground vegetation. We hardly observed fir seedlings in dense herbaceous ground vegetation during our field work. Other studies conducted in Bavarian Limestone Alps on conifers like Spruce have reported dense, smooth ground vegetation to be a serious competitor for the development of spruce seedlings (Bauer 2003; Diaci 2002; in Baier *et al.* 2005).

Though only few studies considered interactions among newly established seedlings, (Tubbs, 1973; in Meredith et al, 1998) demonstrated allelopathic interactions between *Betula lutea* and *Acer saccharum* seedlings. In contrary to this, in the present study a corresponding positive correlation ($P < 0.01$) between fir and other woody seedlings (Table 5) suggests that in general either the seedlings do not occur in close proximity to influence one another significantly or they do not have allelopathic interactions between them.

7.3.4 Altitude

With increasing altitude, tree growth decreases as a consequence of adverse climatic impacts, e.g. low temperature (e.g. Lüscher 1990; in Kupferschmid, 2005). Tree regeneration is not only limited spatially by favorable micro-sites, but also temporally due to irregular seed availability. Seed production is generally lower at higher altitudes compared to lowlands (Mayer and Ott, 1991; Mencuccini *et al.*, 1995 in Kupferschmid *et al.*, 2002) because years with high seed production (i.e. mast years = episodic, synchronized high seed production) become rarer (Mencuccini *et al.*, 1995 in Kupferschmid *et al.*, 2002). In the present study, even though altitude had a significant influence ($P < 0.05$) on the fir seedling occurrence. The meagre significance can be attributed to the fact that differences in altitude were rather small in this study.

7.3.5 Forest Grazing

In Bhutan cattle grazing is a tradition practiced since times immemorial (Norbu, 2000) similar to many parts of the world where forest grazing is practiced (Bland *et al.,* 1994; Etienne, 1996; Roder *et al*; 2002b in Tshering 2005). One of the contributing factors affecting soil physical quality is soil compaction due to trampling (Imhoff *et al.,* 2000) that may affect movement of water and nutrient through soil (Di *et al.,* 2001). In different parts of the world, including Bhutan, studies showed that moderate grazing reduces competition for tree species (Allen and Bartolome, 1989; Gratzer *et al.,* 1999; Norbu, 2000). If the grazing pressure is moderate, cattle do not browse conifer species especially *Abies densa* (Gratzer *et al.,* 1999) due to their high tannin content (Hergert, 1989; Hernes *et al.,* 2000, 2004 in Tshering, 2005). Conifer regeneration especially has been promoted by grazing (Gratzer *et al.,* 1999; Darabant *et al.,* 2007) and to promote regeneration, used as a management tool by reducing competing undergrowth (Gratzer *et al.,* 1999; Norbu, 2000; Tenzin and Rinzin, 2003; Darabant *et al.,* 2007).

At the same time growth of unpalatable shrubs and bushes may be favored as observed in Tsamdrog areas that were invaded by un-palatable shrubs and bushes (RGoB, 2001). In open areas cattle grazing limits the colonization probabilities of woody species (Crawley, 1983 and Seligman, 1996 in Tshering, 2005), and is also documented as a hindrance for forest species seedling survival (Motta, 1996 and Pitt *et al.,* 1998 in Tshering 2005). These findings align with our results, where open areas close to the herding footpath was generally invaded by unpalatable shrubs and bushes like *Rosa sericea, Berberis spp*. At the same time fir seedlings were absent in all the mini-plots near the herding footpath with soil compaction observed in these places. An increasing distance of mini-plots from the migratory herding path led to an increasing probability of fir seedling occurrence.

Nevertheless, Bhutanese farmers and herders have grazing rights (Tsamdrog) in some parts of forests set aside (F&NC Act, 1995, 2005) but grazing is not confined to Tsamdrog only (Norbu, 2000). In general, the regeneration dilemma in conifer forests of Bhutan is the failure of natural regeneration in cleared areas incase *of Abies densa, Picea spinulosa* and *Tsuga dumosa* in western part of Bhutan which warrants special attention.

CONCLUSIONS

Our results suggest that since the dieback, fir (*Abies densa)* seeds have been deposited and germinated, although recruitment during the initial years after the dieback was discontinuous. Some advanced tree regeneration was present in the vicinity of the mini-plots but not inside the mini-plots. At present an average density of 0.6 seedlings of fir per m^{-2} exists. The fact that only 26 percent of the mini-plots showed regeneration indicates patchiness of the regeneration which will result in a mosaic of dense and open forest. Different site factors and other factors, natural and anthropogenic like micro-site (moss, leaf litter, mineral soil and organic matter), grazing, shade, slope, altitude, and competing ground vegetation have influence on *Abies densa* germination and survival. The mortality of *Abies densa* germinants could not be observed. The seedling density of other tree and shrub species like *Juniperus recurva* (0.1 m^{-2}), *Acer sp.* (0.18 m^{-2}), *Rhododendron arboreum* (0.13 m^{-2}), *R. cinnabarinum* (0.11 m^{-2}), *R. lepidotum* (0.18 m^{-2}), *R barbatum* (0.02 m^{-2}), *Viburnum nervosum* (0.01 m^{-2}) and *Rosa sericea* (0.29 m^{-2}), were much lower compared to *Abies densa* (0.6 m^{-2}). These low numbers indicate that it is unlikely that a closed pioneer, *Juniper* or *Acer* stand will be formed, displacing the previous fir stands. For some time, the forest stands will be a mosaic of dense and wide spaced fir trees. We anticipate that over time, mono-specific *Abies densa* forest will eventually once again replace the present stand composition of the dieback affected fir stands.

The results from the present study provide quantitative information about the regeneration status, vegetation dynamics post-dieback and the main factors driving the regeneration in the study area. Since it is the first study in the fir forests of Chamgang, Thimphu in Western Bhutan, there is a large missing information regarding the age of larger trees (most have heart rot), environmental factors like moisture, temperature regimes, rainfall, soil depth, humus and litter thickness, hindrances, under-storey and canopy cover which could have been used to understand the regeneration pattern and vegetation dynamics more better. As it appears from the study that regeneration is driven by a combination of natural and human induced factors, detailed work has to be carried out to understand it more accurately eg. seed production, seed dispersal, establishment, frequency, grazing pattern and intensity. Regarding moss, depending on external input and its status in summers need to be evaluated in future. The studies on mode of seed production, seed and seedlings bank and dispersal should be given emphasis. The regeneration pattern of fir was not very clear from some plots, therefore more study plots should be added below and above the existing permanent plots so that we can clearly differentiate the regeneration patterns emanating from altitude and aspect especially. In respect of aspect and altitude, the information from this study is not precise given the limited number of plots sampled. For example only 3 plots from a total of 20 fell in a different aspect and in the case of altitude; the range of altitudinal difference between the plots is not substantial to make considerable differences in influencing the regeneration.

Our presented data were obtained from both canopy gaps and open areas in the dieback area in which competition of fir with other tree species was either reduced or not present. The effects of different site factors should therefore be evaluated for situations with competition of the tree and shrub species.

One interesting observation made during the study was that one portion of the dieback region is the watershed for streams which feed the population of the lower part of the city downstream.

Even though the dieback occurred more than 30 years before the time of this study, the stand structure in the dieback areas still resemble that of gaps and the species composition in these stands reflect this. The community dynamics (changes in species composition and density) in the study stand should be therefore monitored. Given the limited duration and spatial extent of this study, its results should be carefully interpreted and used in conjunction with other similar study results. Only after convincing and confirming the results through such experiments combined with a long term study, can it provide baseline information that can be used to develop better natural resource management strategies in the region and for determination of future landscape changes.

REFERENCES

1. Allen, B.H., and Bartolome, J.W. (1989): Cattle grazing effects on understorey cover and tree growth in mixed conifer clearcuts.North-West Science, Vol 63, no 5: pages 214-219.
2. Allen, C.D. (2007): Cross-scale interactions among forest dieback, fire and erosion in northern New Mexico landscapes. Ecosystems, 10: 797-808.
3. Allen, C.D. (2009): Climate-induced forest dieback: an escalating global phenomenon? Unasylva 231/232, Vol 60
4. Allen, R.B.; Rose, A.B. (1983): Regeneration of southern rata *(Metrosideros umbellata)* and kamahi *(Weinmannia racemosa)* in areas of dieback. *Pacific Science 37*: 433-442.
5. Anke Jentsch, Jürgen Kreyling, Carl Beierkuhnlein (2007): A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment: Vol. 5, No. 7, pages 365-374.
6. Auclair, A.N.D. (1993): Extreme climatic fluctuations as a cause of forest dieback in the Pacific Rim. Water, Air and Soil Pollution, 66(3-4): pages 207-229
7. Baker, T.T., and Van Lear, D.H. (1998): Relations between density of rhododendron thickets and diversity of riparian forests. Forest Ecology and Management 109. pages 21-32.
8. Baier, R., Meyer, J., Göttlein, A. (2005): Regeneration niches of Norway spruce (*Picea abies* (L.) Karst.) saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps. Eur J Forest Res (2007) 126: 11-22
9. Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., and Zedaker, S.M. (2006): Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighboring vegetation. Forestry 79, 3-27.
10. Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H. (1980, 1998): Forest Ecology. John Wiley & Sons, Inc.
11. Beach E.W. & Halpern C.B. (2001): Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate and vegetation. *Can. J. For. Res.* 31: 471-482.
12. Beckage, B., Clark, J.S., Clinton, B.D., and Haines, B.L (2000): Along term study of tree seedling recruitment in Southern Appalachian forests: The effects of canopy gaps and shrub understories. Canadian Journal Forest Research 30 10, pages 1617-1631.
13. Begon, M., Mortimer, M., and Thompson, D.J. (1996): Population Ecology: A Unified Study of Animal and Plants. Blackwell Science, London: page 247.
14. Brang, P., (1998): Early seedling establishment of *Picea abies* in small forest gaps in the Swiss Alps. *Can. J. For. Res.* 28: (4): 626-639.
15. Brang, P., Moran, J., Puttoten, P., Vyse, A. (2003): Regeneration of *Picea engelmannii* and *Abies lasiocarpa* in high elevation forests of south-central British Columbia depends on nurse logs. Forest Chron 79 (2): 273-279
16. Ciesla, W.M., Donaubauer, E. (1994): Decline and dieback of trees and forests: a global overview. FAO of the UN, Rome,(Italy).FAO Forestry Paper 120: page 90
17. Clark, D.R., and Clark, D.A. (1989): The role of physical damage in the seedling mortality regime of a neotropical rain forest. Oikos 55, pages 225-230.

18. Clary, W.P., and Medin, D. (1990): Differences in vegetation biomass and structure due to cattle grazing in the Northern Nevada Riparian ecosystem. Res.Paper INT.427-USA-FS. 8pages
19. Coates, K.D. (2000): Conifer seedling response to northern temperate forest gaps. Forest Ecol Management 127: pages 249-269.
20. Coates, K.D. (2002): Tree recruitment in gaps of various sizes, clearcuts and undisturbed mixed forest of interior British Colombia, Canada. Forest Ecol Management 155: pages 387-398.
21. Cooper-Ellis S., Foster D.R., Carlton G. & Lezberg A. (1999): Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* 80(8): 2683-2696.
22. Darabant, A., Rai, P.B., Tenzin, K., Roder, W., and Gratzer, G. (2007) : Cattle grazing facilitates tree regeneration in a conifer forest with palatable bamboo understorey. Forest Ecology and Management 252: pages 73-83.
23. Desprrez-Loustau, M.L., Marcias, B., Nageleisen, L.M., Piou, D. & Vannini, A. (2006): Interactive effects of drought and pathogens in forest trees. Annals of Forest Science, 63: 597-612.
24. Di, H.J., Cameron, K.C., Milne, J., Drewry, J.J., Smith, N.P., Hendry, T., Moore, S., and Reijnen, B. (2001): A mechanical hoof for simulating animal treading under controlled conditions, New Zealand Jour.res.44: pages 111-116.
25. Donaubauer, E. (1987): Technical Advisory Services for Forest Development - Draft Report on second part of field studies, Bhutan.
26. Donaubauer, E. (1986): Technical Advisory Services for Forest Development-Bhutan Forest Pathology, FAO (Rome).
27. Donaubauer, E. (1994): On the Decline of Fir (*Abies densa* Griff.) in Bhutan. Institute of Forest Protection, Forest Research Station, Vienna (Austria).
28. Ducey, M.J., Moser, K.W., and Ashton, P.M.S. (1996): Effect of fire intensity on understorey composition and diversity in a Kalmia dominated Oak forest, New England, USA. Vegetation 123: pages 81-90.
29. Duchesneau, R., and Morin, H. (1999): Early seedling demography in balsam fir seedling banks, Canadian Journal of Forests.Res.29, pages 1502-1509.
30. Duncan, R.P. (1991): Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecol 79: pages 1073-1084.
31. Fajvan, M.A., and Wood, J.M. (1996): Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. Forest Ecol and Management 89 (1996): 79-88
32. Forest &Nature Conservation Act, (1995, 2005). Ministry of Agriculture, Thimphu, Royal Government of Bhutan.
33. Forest Resource Develpoment Division (FRDD), DoF (2002): Forestry in Bhutan, Facts and Fifures. In: Department of Forests, Ministry of Agriculture (Ed.).
34. Forest Resource Development Division, DoF/MoA (Bhutan, March 2003): Management Plan for Chamgang – Helela Forest Management Unit, Thimphu Dzongkhag. Period of the Plan: May 1st, 2003 TO April 30th, 2013
35. Fowells, H. A. (1965): Silvics of forest trees of the US. Forest Service Agrri. Handbook Number 271, US Govt. Printing Office, Washington, D.C., USA

36. Frost, P., Medina, E., Menaut, J.C., Solbrig, O., Swift, M., and Walker, B., (Eds) (1986): Responses of Savannas to stress and disturbance. A proposal for collaborative programme of Research. Report of a workshop organized in collaboration with the Commission of European Communities (CEC).Special issue 10, IUBS: pages 1-14
37. Fujihara, M., Hada, Y., Toyohara, G. (2000): Stand structure of Pinus forests affected by pine wilt disease. Proceedings IAVS Symposium, pages: 90-94, 2000.
38. Gillet, F., and Gallandat, J.D. (1996): Wooded pastures of the Jura mountains. In: Western European Silvo-pastoral system Edi. Etienne M.Institut national De la Recherche Agronomique, Paris.
39. Glatzel, G. (1999): Historic forest use and its possible implication to recently accelerated tree growth in Central Europe. In: Karjalainen T, Spieker H, Laroussine O, editors. Causes and Consequences of accelerated tree growth in Europe.EFI proceedings no.27, Joensuu, Finland: EFI, pages 65-74.
40. Gokbulak, F. (1998): Effects of livestock trampling on soil hydro-physical properties, Istanbul Universitesi Orman fakultesi Dergisi 48: pages 113-133.
41. Goreaud, F., Loreau, M., Millier, C. (2001): Spatial structure and the survival of an inferior competitor: a theoretical model of neighbourhood competition in plants. Ecological Modelling.
42. Gratzer, G., and Rai, P.B. (2004a): Density dependent mortality versus spatial segregation in early life stages of *Abies densa* and *Rhododendron hodgsonii* in Central Bhutan .Forest Ecology and Management, Vol 192, Issues 2-3,6thMay 2004: pages 143-159.
43. Gratzer, G., Chhetri, P.B., Rai, P.B., Eckmullner, O. (2004a): Light response of six tree species in the conifer belt of the Bhutan Himalayas. Canadian Journal of Forest Research 34, in press.
44. Gratzer, G., Rai, P.B and Glatzel, G. (1997): Ecology of *Abies densa* Forests of the IFMP – Ura, Bhutan Research Report.
45. Gratzer, G., Rai, P.B. (2002): Structure and regeneration dynamics of *Abies densa* forests in Central Bhutan, Austrian Journal of Forest Science, Oxford No.230
46. Gratzer, G., Rai, P.B; and Glatzel, G. (1999): The influence of the bamboo Yushania microphylla on regeneration of *Abies densa* in central Bhutan. Canadian Journal of Forest Research.29: pages1518-1527.
47. Gray, A.N., and Spies, T.A. (1997): Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78: pages 2458-2473.
48. Greeene, D.F. (1999): A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forests Res.29, pages 824-839
49. Grierson, A.G.C., and Long, D.C. (1983): Flora of Bhutan, Vol 1, Part 1.Royal Botanic Garden, Edinburgh (UK).
50. Grubb P.J. (1977): The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.
51. Grubb, P.J. (1977): The maintenance of species richness in plant communities: the importance of regeneration niche. Bio.Rev 52, pages 107-145
52. Gyeltshen, N. (2008): Regeneration ecology of Broadleaved Forests of Bhutan; Effect of Strobilanthes competition on tree regeneration. Institute of Forest

Ecology. University of Natural Resources and Applied Life Sciences, BOKU, Vienna.

53. Hale, S. (2004): Managing light to enable natural regeneration in British Conifer Forests, Forestry Commission, UK.
54. Hansen A.J., Garman S.L., Weigand J.F., Urban D.L., McComb W.C. Harmon, M.E., and Franklin, J.F. (1989): Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70: pages 48-59.
55. Harper, J.L. (1977): Population Biology of Plants. Academic Press, New York.
56. Herrera, C.M., Jordano, P., Lopez-Soria, L., and Amat, J.A. (1994): Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivoro activity and seedling establishment. Ecol Monogr.64: pages 315-344.
57. Hibino, K., Sato, K., Iwata, H. & Izumi, S. (1981): An ecological study on the *Abies mariesii* seedling. In: *Ecological Studies on the Abies mariesii Forest* (ed. S. Iizumi) pp. 1-14. The Mount Hakkoda Botanical Laboratory, Tohoku University, Sendai (in Jap with English summary).
58. Hicke, J.A., Logan, J.A., Powell, J., & Ojima, D.S. (2006): Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in Western US. Journal of Geophysical Research, 111: G02019.
59. Hogget, A. (2000): Western hemlock looper and forest disturbance in the ICHwk3 of the Robson Valley; Stage 2: The Effects of western hemlock looper - Report and silviculture recommendations. Faculty of Forestry, University of British Columbia**.**
60. Holsten, E.H., Werner, R.A., & Develice R.L. (1995): Effects of a spruce beetle (*Coloptera: Scolytidae*) outbreak and fire on Lutz spruce in Alaska. *Env. Entomol.* 24(6): 1539-1547.
61. Hubbard, W., Christopher, Latt., Long, A. (1998): Forest Terminology for Multiple Use Management. In. Institute of Food and Agricultural Sciences, University of Florida
62. Huffman, D.W., Tappeiner II, J.C., and Zasada, J.C. (1993): Regeneration of Salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. Canadian Jour. Bot. 72: pages 39-41.
63. Inderjit and Mallik, A.U. (2002): Can *Kalmia angustifolia* interefere to Black Spruce (*Picea mariana*) be explained by allelopathy? Forest Ecology and Management, Vol 160, Issues 1-3: pages 75-84.
64. Inhoff, S., Silva, A.P., and Tormena, C.A. (2000): Applications of the resistance curve in the control of the physical quality of soils under grass, Pesquisa Agropecuaria Brasileira 35, pages 1493-1500.
65. Janzen, D.H. (1976): Why bamboos wait so long to flower. Ann. Rev. Ecol Syst.7, pages 347-391
66. Jump, A., Hunt, J.M. & Penuelas, J. (2006): Rapid climate change related growth decline at the southern range edge of *Fagus sylvatica*.Global Change Biology, 12: 2163-2174.
67. Keddy, P.A. (2001): Competition.Kluwer Academic Publishers.
68. Kirisits, T., Donabauer, E., Konrad, H., Barnes, I., Maier, W., Wingfield, M.J., Gyeltshen, N., Chhetri, D.B. (2007): Common Needle, Shoot, Branch and Stem

Diseases of Conifer Trees in Bhutan. Acta Silv. Lign. Hung., Spec. Edition (2007), 241-245

69. Knapp, A.K., and Smith, W.K. (1982): Factors influencing understorey seedling establishment of Engelmann Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocara*) in Southeast Wyoming. Canadian Journal of Botany 60: pages 2753-2761.
70. Knoke, T. (2003a): Predicting red heartwood formation in beech trees (*Fagus sylvatica* L). Ecol Model 169: 295-312
71. Krebs, C.J. (2001): Ecology. Addison Wesley Longman.
72. Kupferschmid, A.D. (2005): Succession in a protection forest after *Picea abies* dieback. A dissertation submitted to the Swiss Federal Institute of Technology, Zurich for the degree of Doctor of Natural Sciences. DISS. ETH NO. 15228
73. Kupferschmid, A.D., Bugmann, H.: Effect of microsites, logs and ungulate browsing *on Picea abies* regeneration in a mountain forest. Forest Ecology and Management 205 (2005) 251–265
74. Kupferschmid, A.D., Schönenberger, W., and Wasem U. (2002): Tree regeneration in a Norway spruce snag stand after tree die-back caused by *Ips typographus*. *For. Snow Landsc. Res.* **77**(1/2): 149-160.
75. Lambers, H., Chaplin III, F.S., and Pons, T.L. (1998): Plant Physiological Ecology.Springer, Berlin.
76. Lässig, R., & Motschalow, S.A. (2000): Frequency and characteristics of severe storms in the Urals and their influence on the development, structure and management of the boreal forests. *For. Ecol. Manage.* 135: 179-194.
77. LePage, P.T., Canham, C.D., Coates, K.D., and Bartemucci, P. (2000): Seed abundance versus substrate limitation of seedling recruitment in Northern temperate forests of British Colombia. Canadian Journal of Forest Research 30, pages 415-427.
78. Louw, J.H. (1995): Site classification and evaluation for commercial forestry in the Crocodile river catchment, Eastern Transvaal. Unpublished M.Sc Thesis. Faculty of Forestry, University of Stellenbosch, Stellenbosch: page 331.
79. LUPP, (1995): LUPP Dzongkhag data sheets for Bhutan, Land Use Planning Project, MoA, Thimphu, Bhutan.
80. Meredith, W., Cornett, Klaus J. Puettmann, and Peter B. Reich (1998): Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. Can. J. For. Res. 28(2): 196–205 (1998)
81. Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., Lechkowitz, M.J. (1999): Functional ecology of advance regeneration in relation to light in boreal forests. Canadian Journal of Forest Research 29, pages 812-823
82. Morin, P.J. (1999): Community Ecology. Blackwell Science, New Jersey.
83. Mueller, D., Dombios. (1985): ’Ö’hi’a Dieback in Hawaii. Pacific Science, Vol39, no 2
84. Mueller-Dombios, Dieter. (1991): Stand demography and vegetation change. Coenoses 6: 139-141
85. Mueller-Dombios, Dieter. (1991): The mosaic theory and spatial dynamics of natural dieback and regeneration in Pacific forests. In: Remmert T(ed) The

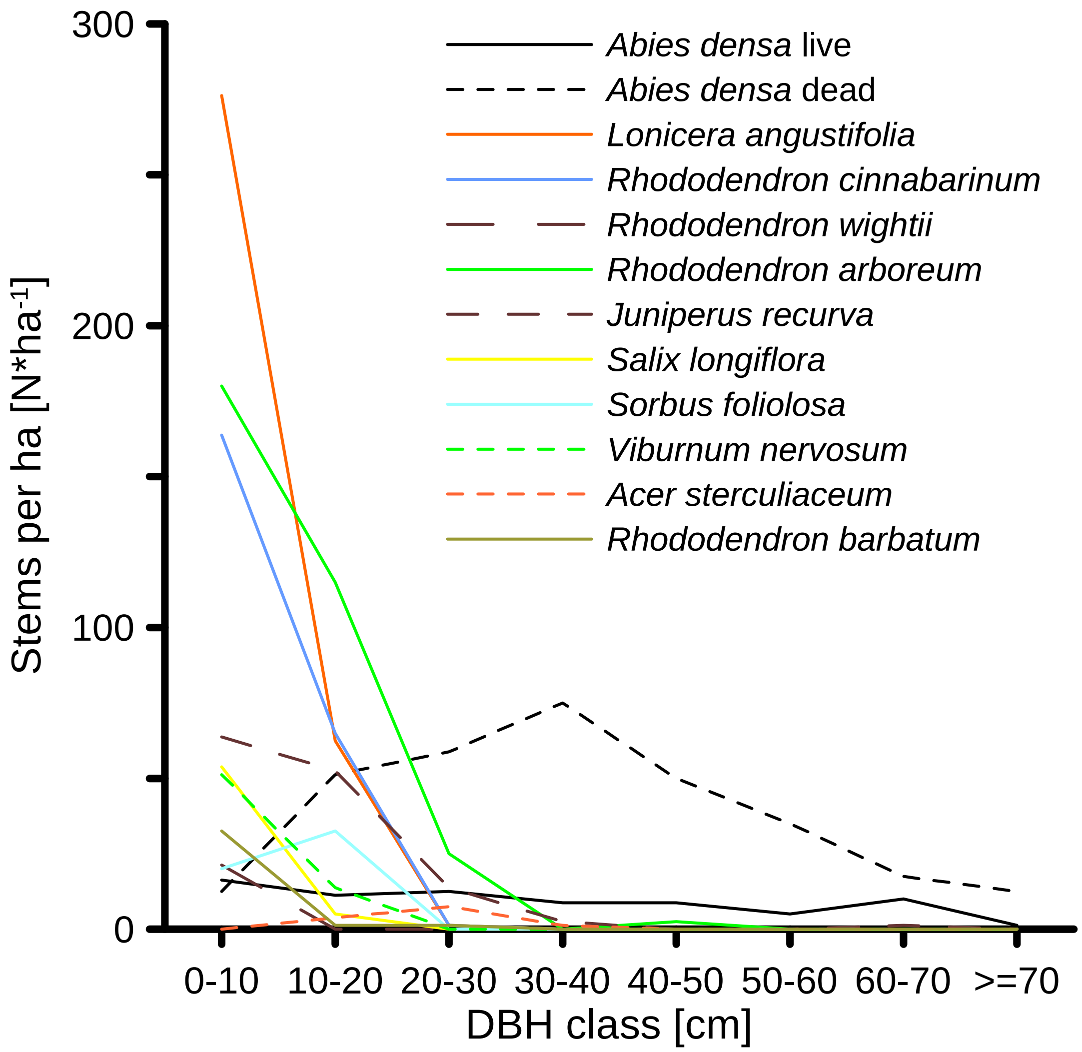
mosaic-cycle concept of ecosystem. Springer, berlin Heidelberg, New York, pages 46-60
86. Mwendera, E.J., and Saleem, M.A.M. (1997): Hydrologic response to cattle grazing in the Ethiopian highlands, Agri Ecosystem Environ.64: pages 33-41.
87. Nagaike, T.(2003): Edge effects on Stand Structure and Regeneration in Subalpine Coniferous Forest on Mt.Fuji, 30 Years after Road Construction. Arctic, Antartic, and Alpine Research, Vol. 35, No.4, 2003, pages: 454-459.
88. Nakamura, T. (1990): Succession and regeneration of subalpine forests in central Japan. Jpn. J. Hist. Bot. 7: 3-14 (in Jap with English summary).
89. Nakamura, T. (1992): Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan.Ecological Research 7, 155-162
90. Nakashizuka, T. (1998): Regeneration of Beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*).Ecological Research 3: pages 21-35.
91. Nilsen, E.T., Clinton, B.D., Lei, T.T., Miller, O.K., Semones, S.W., and Walker, J.F. (2001): Does rhododendron maximum L.(Ericaceae) reduce the availability of resources above and below ground for canopy tree seedlings. Am. Midl. Nat.145, pages 325-343.
92. Nilsen, E.T., Walker, J.F., Miller, O.K., Semones, S.W., Lei, T.T., and Clinton, B.D. (1999): Inhibition of seedling survival under Rhododendron maximum (Ericaceae): Could allelopathy be a cause? Am. Jour.Bot.86 11, pages 1597-1605.
93. Norbu, L. (2000): Cattle grazing-An integral of broadleaf forest management planning in Bhutan. Ph.D dissertation, ETHZ. Zurich, Switzerland.
94. O'Connor (1995): Acacia karroo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment, Oecologia 103: pages 214-223.
95. Oosting, H.J., Kramer, P.J. (1946): Water and light in relation to pine reproduction. Ecology 27, pages 47-53
96. Oshima, Y. (1961): Ecological studies of *Sasa* communities. I: Productive structure of some of the *Sasa* communities in Japan. Bot. Mag. Tokyo 74: 199-210
97. Peterken, G.F., and Tubbs, C.R. (1965): Woodland regeneration in the New Forest Hampshire since 1650.Journal of Appl.Ecol.2: pages 159-170.
98. Peterson, C.J., and Pickett, S.T.A. (1990): Microsite and elevational influences on early forest regeneration after catastrophic windthrow.Journal of Veg.Science 1: pages 657-662.
99. Pouliot, D.A., King, D.J., and Pitt, D.G (2006): Automated Assessment of Hardwood and Shrub Competition in regenerating forests using leaf-off airborne imagery. Science Direct.
100. Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., & Romme, W.H. (2008): Cross scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions.Bioscience,58 (6): 501-517.
101. Rey, P.J., Alcantra, J.M. (2000): Recruitment dynamics of a fleshy fruited plant (*Olea europea*): connecting patterns of seed dispersal to seedling establishment, Journal of Ecology 88, pages 622-633.

102. Robert, J.(Roj) Miller.(1997): Natural regeneration of Spruce, Ministry of Natural Resources, Forest Management Branch, Forest Evaluation and Standards Section 99,Foster Drive, Suite 400 Sault Ste. Marie, Ontario, Canada P6A.
103. Roder, W., Dorji, K., Gratzer, G. (2003): Nutrient flow from the forest-source of life for traditional Bhutanese agriculture.
104. Roder, W., Wangdi, K., and Gyamtsho, P. (2001): Feeding the Herbs: Improving Fodder Resources in Bhutan. ICIMOD, Kathmandu (Nepal).
105. Ross, D.W., Daterman, G.E., Boughton, J.L., & Quigley, T.M. (2001): Forest health restoration in south-central Alaska: a problem analysis. *Gen. Tech. Rep. USDA For. Serv.* PNW-GTR-523: 1-38.
106. Rosset, J. (1999): Temperate conifer forests of Bhutan.In, RNR-RC Jakar Special Publication, Bumthang (Bhutan): page 95.
107. Royal Government of Bhutan (2001): Proceedings of the National Grazing Policy Workshop, Ministry of Agriculture. August 21-24, 2001
108. Sakamoto, K., Miki, N., Tsuzuki, T., Nishimoto, T., Yoshikawa, K. (2003): Comparison of stand dynamics after dieback caused by pine wilt disease among pine forests with different management regimes in western Japan. J For Res (2003) 8: 303-309.
109. Schulz, B. (1996): Response of residual spruce in beetle-impacted stands in Resurrection Creek Drainage, Kenai Peninsula, Alaska. *USDA Forest Service Technical Report*-62. 21p.
110. Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J. & Naik, N. (2007): Model projections of an imminent transition to a more arid climate in southwestern North America,Science,316:1181-1184.
111. Stanturf, J.A., Schoenholtz, S.H., Schweitzer, C.J., and Shepard, J.P. (2001): Achieving restoration success: Myths in bottomland hardwood forests.Restor.Ecol.9: pages 189-200.
112. Stanturf, J.A., Schweitzer, C.J., and Gardiner, E.S. (1998): Afforestation of marginal agricultural land I the Lower Mississippi River Alluvial Valley, USA. Silva Fenn.32: pages 281-297.
113. Stilling, P. (1996): Ecology-Theories and Applications. Prentice Hall International.
114. Sugita, H., Tani, M. (2001): Differences in microhabitat-related regeneration patterns between two subalpine conifers, *Tsuga diversifolia* and *Abies mariesii* on Mount Hayachine, Northern Honshu, Japan. Ecological research 16: pages 423-433.
115. Swetnam, T.W., and Betancourt, J.L. (1998): Mesoscale disturbances and ecological response to decadal climatic variability in the American Southwest. Journal of Climate, 11: 3128-3147.
116. Takada, T., and Nakashizuka, T. (1996): Density dependent demography in a Japanese temperate broad-leaved forest. Vegetation 124: pages 211-221
117. Takahashi, K., Uemura, S., Suzuki, J.-I., and Hara, T. (2003): Effects of understorey dwarf bamboo on soil water and the growth of overstorey trees in dense secondary Betula ermanii forest, Northern Japan. Ecological Research 18: pages 767-774.

118. Tappeiner, J., Zasada, J., Ryan, P., and Newton, M. (1991): Salmonberry clonal and population structure: The basis for a persistent cover. Ecology 72 2: pages 609-618.
119. Taylor, A.H., and Qin, Z. (1988a): Regeneration patterns in old growth Abies-Betula forests in the Wolong Natural Reserve, Sichuan, China. Journal of Ecol.76, pages 1204-1218.
120. Taylor, A.H., and Qin, Z. (1988b): Regeneration from seed *of Sina arundinaria fangiana*, a bamboo in the Wolong Giant Panda Reserve, Sichuan. China.Journal of Bot.75, pages 1065-1073.
121. Tenzin, K. (2008): Regeneration and gap dynamics in mixed conifer forests of Bhutan Himalayas. Institute of Forest Ecology, University of Natural Resources and Applied Life Sciences, Vienna (Austria).
122. Tenzin, K., and Rinzin. (2003): Impact of livestock grazing on regeneration of some major species of plants in conifer forests. In. RNR-RC, Jakar, Bumthang, Bhutan.
123. Thomas, P., Rooney, Donald M. Waller.(1998): Local and regional variation in hemlock seedling establishment in forests of the upper Great lakes region, USA, Forest Ecology and Management 111(1998),pages 211-224.
124. Tilman, D. (1986): Mechanisms of Plant Competition.In: Crawley, M.J. (Ed.), Plant Ecology. Blackwell Science.
125. Timoney, K.P. & Peterson, G. (1996): Failure of natural regeneration after clearcut logging in Wood Buffalo National Park, Canada. *For. Ecol. Manag.* 87(1-3): 89-105.
126. Tshering, P. (2005): The Interaction of Grazing and Competition in the Conifer Forest of Bhutan. Institute of Forest Ecology. University of Natural Resources and Applied Life Sciences, BOKU, Vienna.
127. Ulanova, N.G. (2000a): The effects of windthrow on forests at different spatial scales: a review. *For. Ecol. Manage***.** 135: 155-167.
128. Veblen, T.T. (1982): Growth patterns of Chusquea bamboos in the understorey of Chilean Nothofagus forests and their influences in forest dynamics. Bull.Torrey Bot.Club 1094, pages 474-487.
129. Veblen, T.T., Hadley, K.S., Reid, M.S., & Rebertus, A.J. (1991): The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecol.* 72: 213-231.
130. Villalba, R., and Veblen, T.T. (1998): Influences of large scale climatic variability on episodic tree mortality in Northern Patagonia. Ecology 79: pages 2624-2640.
131. Wangchuk, K. (2007): Natural regeneration ecology of mixed conifer forests in Western Bhutan. Institute of Forest Ecology. University of Natural Resources and Applied Life Sciences, BOKU, Vienna.
132. Wangchuk, S. (2002): Grazing Management in Protected areas. Journal of Bhutan Studies 7.
133. Wardman, C.W., and Schmidt, M.G. (1998): Growth and form of Douglas fir adjacent to persistent vine maple gaps in South-Western British Columbia. Forest Ecol. Management 106 2-3: pages 223-233

134. White, P.S and Pickett, S.T.A. (1985): Natural disturbance and patch dynamics: An introduction in the ecology of Natural disturbance and Patch Dynamics, edited by S.T.A.Pickett and P.S.White.Academic Press, New York, pages 3-13.
135. Wood, J.C., Blackburn, W.H., Pearson, H.A., and Hunter, T.K. (1989): Infiltration and runoff water quality response to silvicultural and grazing treatments on a longleaf pine forest. Jour. Range Manage.42: pages 378-381.
136. Yamamoto, S., Nishimura, N., and Matsui, K. (1995): Natural disturbance and tree species coexistence in an old growth beech -dwarf bamboo forest, SW Japan. J. Veg. Sci. 6, pages 875-886.
137. Zheng, Daolan., Wallin, D., Hao, Z. (1997): Rates and patterns of landscape change between 1972 and 1988 in the Changbai Mountain area of China and N Korea. Landscape Ecol 12: 241-254

Appendix 1: DBH Class distribution of different tree and shrub species in the study area



Appendix 2: DBH Class-Height Curve of Fir (*Abies densa*)

Fit Results

Fit 1: Log
Equation Y = 6.222196607 * ln(X) - 7.05816468
Number of data points used = 59
Average ln(X) = 3.07655
Average Y = 12.0847
Residual sum of squares = 340.913
Regression sum of squares = 1832.66
Coef of determination, R-squared = 0.843156
Residual mean square, sigma-hat-sq'd = 5.98093