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**LONG-TERM FOREST DYNAMICS:
PERMANENT PLOT DATA FOR MODELLING**

**METSADE PIKAAJALINE DÜNAAMIKA:
PÜSIKATSEALADE ANDMESTIK MODELLEERIMISEKS**

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, references in the text are made by their Roman numerals. The papers are reproduced by kind permission of the publishers.

- I Shorohova, E., Kuuluvainen, T., **Kangur, A.**, Jõgiste, K. 2009: Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science*, 66, 2 (201): 1-20.
- II **Kangur, A.**, Korjus, H., Jõgiste, K., Kiviste, A. 2005: A conceptual model of forest stand development based on permanent sample-plot data in Estonia. *Scandinavian Journal of Forest Research*, 20 (Suppl. 6): 94-101.
- III Sims, A., Hordo, M., **Kangur, A.**, Kiviste, K., Jõgiste, K., Gadow, K.v. 2009: Tracking disturbances induced changes in stand development on irregular measurement intervals in the Järvelja forest experiments. *Baltic Forestry*, 15 (2): xx-xx (Accepted manuscript 15. 06. 2009)
- IV **Kangur, A.**, Sims, A. Jõgiste, K., Kiviste, A., Korjus, H., Gadow, K.v. 2007: Comparative modeling of stand development in Scots pine dominated forests in Estonia. *Forest Ecology and Management*, 250 (1-2): 109-118.
- V Padari, A., Metslaid, S., **Kangur, A.**, Sims, A., Kiviste, A. 2009: Modelling stand mean height in young naturally regenerated stands – a case study in Järvelja in Estonia. *Baltic Forestry*, 15 (2): xx-xx (Accepted manuscript 15. 06. 2009)

The contributions from the authors to the papers are as follows:

Paper	Original idea and structure of paper	Data, methods and study design	Data collection	Data analysis	Preparation of manuscript
I	ES, TK	ES, TK	ES, TK, AK	All	All
II	AK , HK	All	AK , KA	AK , KA	All
III	KA, AK , AS	AK , AS, KA	AK , AS, KA, MH	AS, AK	All
IV	AK , AS	AK , AS	AK , AS, KA	All	All
V	AK , KA	KA, AK , AP	AK , AP, SM	All	All

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ABBREVIATIONS

ENFRP	The Estonian forest research plots network
JLTFE	Järvelja long-term forest experiments
NOLTFOX	Northern European Database of Long-term Forest Experiments
D	Tree diameter
IPCC	Intergovernmental Panel of Climate Change
cN_x	The accumulated number of trees
N_x	Number of trees at the enumeration period i
t	Measurement interval (years)
NG	The weight of a disturbance, ratio between removed and total number of trees (rN) and removed and total basal area (rG)
rG	Ratio between removed (G_{ibn}) and total basal area (G_{tot})
rN	Ratio between removed (N_{ibn}) and total number of trees (N_{tot})
N_{ibn}	Removed number of trees
N_{tot}	Total number of trees
G_{ibn}	Removed basal area
G_{tot}	Total basal area

1. INTRODUCTION

There are challenges involved in modelling of ecological dynamics. For describing forest succession it is necessary to understand and to integrate processes that operate from instantaneous scale to generational into the modelling. The disturbance processes can span from seconds (effect of fire or extreme winds) to centuries (decomposition, soil formation) (Perry & Millington, 2008). The empirical data about long-term dynamics is collected during forest inventories and long-term experiments. However, matching forestry data to forest stand and ecosystem long-term dynamics is uncommon. Such a method has a great potential for more comprehensive modelling of vegetation dynamics. Particularly important is the inclusion of individual tree observations that enables the tracking of causes for dynamic forest stand pattern (e.g., separating competition-induced self-thinning from effects of an allogenic disturbance agent).

Studies on long-term vegetation dynamics are often conducted using chronosequences (Brubaker, 1981). With this method generally the long-term sequence of re-measurements in time are substituted by point measurements in space with the assumption of “similar environments” at different ages. The use of this information in long-term modelling is sometimes difficult, as it contains unexplained variation components (Bakker et al., 1996). For the study of disturbance dynamics, chronosequences do not give the needed information about the history of the factors altering the system, about the responses of the community or describe the change rates of these influencing variables. A contrasting approach is using permanent sample plots for long-term study of dynamics at the same spot. A compromise between chronosequences and permanent plots that was proposed by Gadaw & Hui (1999) as interval measurements where the study points (plots) are measured at least twice for collecting the information about the dynamics of variables of particular interest. The data gathered from long-term studies, including both observational and experimental investigations, can be used to formulate hypotheses on the mechanisms of species dynamics during various successional stages. Empirical time series have been proven to be of critical value to study disturbance dynamics, but their logistical limitations set boundaries on more widespread use of this method (Myster & Malahy, 2008).

Natural ecosystems and communities are characterized by two main features. First, they are dynamic systems and, second, their spatial distribution is heterogeneous (Sousa, 1984). The dynamic nature of a forest ecosystem structure has been widely acknowledged (Oliver & Larson, 1996; Frelich, 2002; Stanturf, 2004). On a larger spatial scale sometimes a self-perpetuating steady state may exist (Clements, 1936). However, in the majority of ecosystems a major disturbing shift (disturbance) often occurs before the community reaches equilibrium status. The spatial heterogeneity (pattern) is itself dynamic, since environmental characteristics and population properties are changing with time (Sousa, 1984; Oliver & Larson, 1996).

In forest succession, disturbance is a major source of spatial and temporal heterogeneity (Oliver, 1980; Sousa, 1984). When applying natural disturbance concepts to stand development modelling or forest restoration and management practices, spatial and temporal scaling becomes important (Jørgiste et al., 2007). Disturbances operate at multiple spatial scales and often disturbances at different scales interact, producing multi-scale habitat diversity, from microhabitats to landscape patterns (Lertzman & Fall, 1998). Within the framework of disturbance dynamics, there are two equally important characteristics, disturbance return interval (frequency) and disturbance magnitude (Pickett & White, 1985). There are ecosystems where small and frequent disturbances may have effects similar to the effects of large infrequent disturbances. Any ecosystem has internal mechanisms of resistance to the disruptive effects of disturbances (Romme et al., 1998). If such natural resilience mechanisms are overwhelmed disturbance may change to degradation (Stanturf, 2004).

Climate change is a global issue that has been extensively studied and recognized (McCarthy et al., 2001). Often global change is perceived as human-induced atmospheric modifications. In studying the processes in forest ecosystems, cumulative and complex effects of environmental changes should be considered, including global climate change but also human-induced land use changes (Hansen et al., 2001). Climate directly affects disturbance regimes through the abiotic disturbance agents (Zackrisson et al., 1995), and has an indirect impact through the activity periods of biotic disturbance agents. The changes in climate affect forest disturbance agents, frequency, intensity and magnitude. For example in northern North-America, the cascading effects of warming climate have

shortened the recovery period between consequent spruce bark beetle outbreaks, resulting in massive outbreaks (Berg et al., 2006).

Almost all boreal and hemiboreal forests have been affected by humans directly (managed) (Dale et al., 2001) or indirectly (atmospheric changes). The conversion of natural vegetation to urbanized or anthropogenic land types may change the disturbance frequency and magnitude. Commercially managed forests of uniform stands with simplified structure are subject to more severe disturbance effects than stands with natural structures.

Climate and land use change interactions affect biodiversity in general, modifying species distribution, changing dispersal routes, or shifting natural barriers of invading species or pests (Hansen et al., 2001). All species living in anthropogenic sites originating from natural sites have developed specific adaptations that differ from naturally dynamic environments (Jögiste et al., 2007). Unpredictable disturbance regimes under a changing climate will present an extreme test to these adaptations. Therefore all means in forestry are needed in supporting these natural resilience links (Niemelä et al., 2001).

Ecosystem management assumes that management practices based on natural disturbance patterns will most likely preserve both natural biodiversity and ecosystem functions (Grumbine, 1994; Pavlikakis & Tsihrintzis, 2000). Ecosystem management therefore combines traditional natural resource management and forestry practices with classical conservation management in order to focus on sustaining natural ecosystem development. Increased knowledge and understanding of natural disturbance dynamics in boreal and hemiboreal forests allows us to develop a template for sustainable forest management based on mimicking natural disturbances that are the means to contribute to biodiversity of the ecosystem. Near-natural silviculture, also widely practiced in Estonia, uses site adapted native species and management paths mimicking natural disturbances and enables a high degree of naturalness even in intensively managed forests (Korjus, 2009).

In traditional forestry, forest management and modelling is based on regular management schedules developed for specific forest types and assumed as optimal for given site conditions. Such uniform silviculture creates standardized forest stands, which ignore spatial and temporal

aspects and that are inflexible if conditions change. New methods in forest management planning (Gadow et al., 2007; Gadow et al., 2008; Kangas et al., 1996) enable realistic individual simulation of growth, disturbance regimes and harvest events of stands as well as considering all available data and multiple objectives in forest ecosystem management. In such a way, tree or stand level data and models are translated to individualized landscape level decisions considering all specific aspects of ecosystem management.

2. REVIEW OF LITERATURE

2.1. Environmental conditions, tree species and the classification of Eurasian boreal and hemiboreal forest ecosystems

The main climatic factors determining forest growth in boreal and hemiboreal zone are temperature regime and length of growing season. The climate is characterized by long cold winters and short, warm and sunny summers. Low temperature and frost during winter affects all aspects of life and nutrient cycling in below- and aboveground. The mean annual temperature and precipitation are low. Depending on the latitude, maritime-continentiality gradients, and local topography a considerable variation exists. In continental areas such as central Siberia, winter temperatures fall to -50°C . The mean temperature in July varies between 10°C and 22°C . Annual precipitation varies between 300 and 600 mm (**Paper I**). In the European boreal forest, Atlantic influence and cyclones result in a milder climate with more rain and instability than in the continental regions of Eurasia (Hytteborn et al., 2005).

The footprints (lakes and bogs formed in landscapes scraped by glaciers) of the last glacial period over 10,000 years ago are clearly visible in the boreal region (Jögiste et al., 2008). Soil formation is characterized by podzolization processes: the acidic reaction of decomposing litter causes leaching and moving of minerals in topsoils, resulting in a light horizon below the forest floor and deposition of humic materials and iron oxides in the subsoil (**Paper I**). Under conditions of a positive precipitation–evapotranspiration balance, a fine-grained pattern of lowland forests and wetlands forms (Hytteborn et al., 2005). The effect of low decomposition rates, due to low soil temperatures together with poor drainage, leads to humus and peat accumulation. In the northernmost areas with the lowest mean annual and winter temperatures, permafrost prevails. Forests can grow where the permafrost melts to a depth of 1 m during the growing season. The presence of permafrost also leads to the development of palsas and peat plateaus (Bhiry et al., 2007).

The boreal forest is dominated by coniferous species belonging to *Abies* (mainly *A. sibirica* Ledeb.: Siberian fir), *Larix* (mainly *L. gmelinii* (Rupr.) Rupr.: Dahurian larch, *L. sibirica* Ledeb.: Siberian larch, *Picea* (mainly *P. abies* (L.) H. Karst.: Norway spruce, *P. obovata* Ledeb.: Siberian spruce) and *Pinus* (mainly *P. sylvestris* L.: Scots pine, *P. sibirica* Du Tour or (Loudon) Mayr.: Siberian pine) genera.

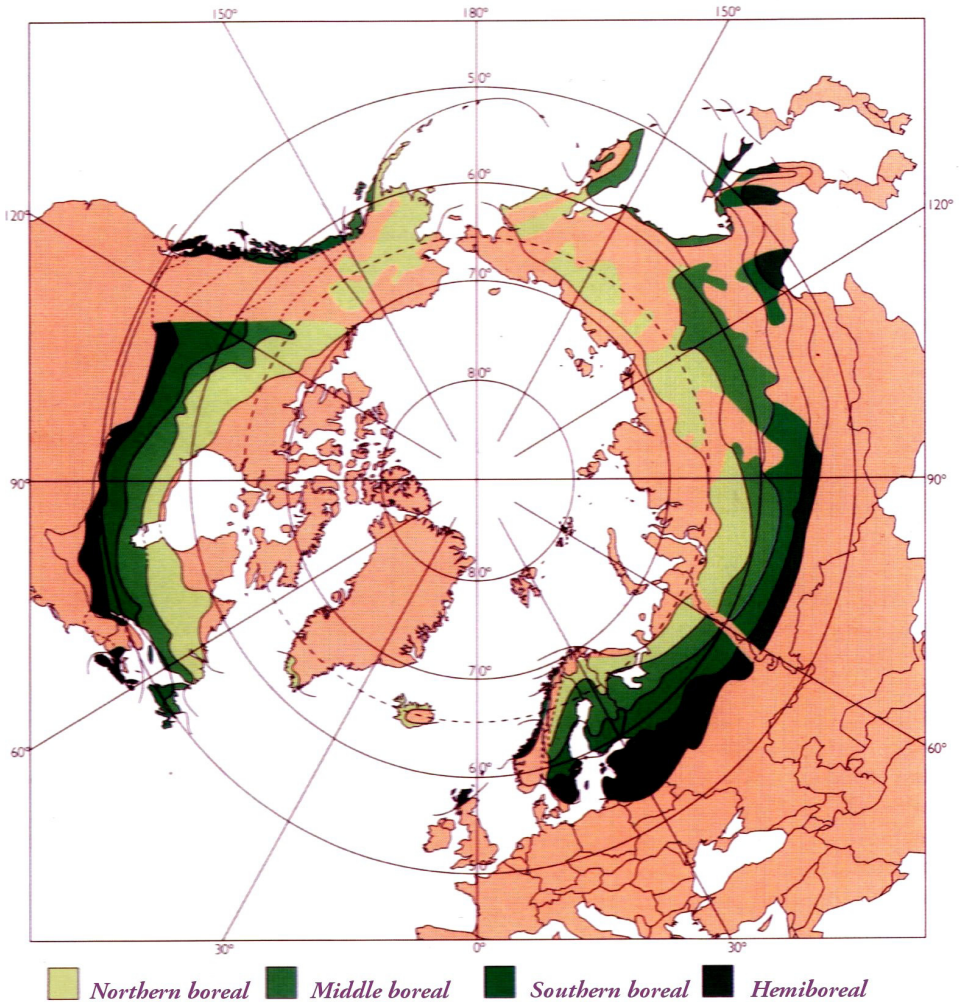


Figure 1. The extent of boreal and hemiboreal forest. Based on Mönkkönen (2004).

In the southern parts of boreal forest and in hemiboreal regions deciduous species (*Betula pendula* Roth.: silver birch, *B. pubescens* Ehrh.: downy birch, *Populus tremula* L.: aspen, *Alnus incana* (L.) Moench.: grey alder, *A. glutinosa* (L.) Gaertn.: black alder) are present and forming admixtures with coniferous species.

Several studies in Northern Eurasia and North America have described the regional variation within the boreal forest biome (Spribille & Chytrý,

2002). Different biotic zonation schemes (classifications of vegetation zones) have been worked out for the boreal zone. One widely recognized scheme was developed by Ahti et al. (1968), identifying the *hemiboreal*, *southern*, *middle* and *northern boreal* vegetation zones (Figure 1) (Essen et al., 1997; Mönkkönen, 2004).

The southernmost transition area between boreal and temperate (nemoral) regions is classified as boreonemoral or hemiboreal zone (Figure 1). It is characterized by coniferous species dominating in admixtures with temperate hardwoods, including pedunculate oak (*Quercus robur* L.), ash (*Fraxinus excelsior* L.), European white-elm (*Ulmus laevis* Pall.), Wych elm (*U. glabra* Huds.), beech (*Fagus sylvatica* L.), Norway maple (*Acer platanoides* L.), lime (*Tilia cordata* Mill.) and dominance of large number of herbs in the ground vegetation (Ahti et al., 1968; Essen et al., 1997; Spribille & Chytrý, 2002).

The occurrence of abovementioned broadleaved trees diminish gradually towards the north in the southern boreal zone. Both the middle and northern boreal zones are conifer dominated (Dahurian larch, Siberian spruce, and Scots pine) having only birch (*Betula pubescens* ssp. *tortuosa*) as the main hardwoods there (Hyttborn et al., 2005).

Ecotones among the northern coniferous forests are delineated by mountains or grasslands. In the north the boreal forest undergoes a transition with the tundra vegetation type. The ecotone of the forest-tundra is a belt between the taiga and treeless tundra (**Paper I**).

2.2. Successional dynamics of forest ecosystems

Forest ecosystems are dynamic, subject to natural developmental processes as well as natural and anthropogenic stresses and disturbances (Stanturf, 2004). The forest ecosystems can be explained through three attributes: 1) *composition*, 2) *function* and 3) *structure*. Composition describes the proportion and presence of different species. Function can be explained as “work” carried out by ecosystem. This includes many different processes like nutrient transport and production, gas and hydrologic cycles and others. Forest ecosystem structure describes the individual structural variability itself; but it also includes the spatial location of these structures throughout the ecosystem (Franklin et al., 2002). Worldwide the changing

behaviour of these attributes is as well recognized as the importance of understanding their effect to the successional development (Bormann & Likens, 1979; Oliver, 1980).

Complete conceptual models of forest development are needed for guiding forest resource management planning. Widely recognized and suggested is that the best and accurate models, that satisfy all three ecosystem attributes, should be constructed following studies from natural forest stands (Franklin et al., 2002). Following the classical Clementsian conceptual approach (Clements, 1916), forest dynamics proceeds through serial basic community changes before reaching to the steady climax phase (Clements, 1936). The generalized theoretical models, including stand development and succession, have been developed and suggested by Bormann & Likens (1979) and Peet & Cristensen (1987). Well known and widely cited are stand structure models created by Oliver (1980) and Oliver & Larson (1996).

The stand development concept has been later adapted and developed by many of forest development classification schemes (Spies & Franklin, 1996; Carey & Curtis, 1996). Later on these basic schemes for forest ecosystem development and succession were merged with the concept of forest disturbance regimes by Frelich (2002) and Franklin et al. (2002) including three basic process-based stages and a fourth structural condition: (1) The stand initiation stage; (2) stem exclusion stage; (3) the demographic transition phase; (4) the old multi-aged phase.

2.3. Models of successional dynamics

The models of succession have been developing together with the growing information on forest ecosystem development. The aim has been providing simple descriptions for understanding forest structure and composition changes (Kimmins, 1987) for predicting future states of populations in contemporary forest management decision support tools (Kimmins et al., 2008).

The distinction between the succession types following the change incentive are: 1) autogenic succession, describing the system changes with internal origin (e.g., self-mortality prediction model) and 2) allogenic succession, where the changes are originating outside the observable system

(e.g., descriptive model of stand compositional changes caused by grazing mammalian herbivores) (Kimmins, 1987).

Based on the methodological setup the models of succession are separated to be empirical or theoretical. The most fundamental modelling type has been the creation of theoretical conceptual models (Kimmins, 1987), where the cause-effect chain is followed or the process of change is described. These classical concepts of succession at community replacement level presented by Clements (1916), Odum (1969), and later on species replacement level by Gleason (1923) and Connell & Slatyer (1977), have been initially constructed theoretically and then followed by the empirical testing and validation. The empirical models (or experience-based models) of populations and communities, created based on field measurements or observations in the past, tend to describe the successional changes in ecosystem level (Kimmins et al., 2008).

In the classification of forest dynamic models presented by the Shugart & West (1980) the basic organizational categories follow the modelling unit: individual tree level, small patch or gap level and on stand level. Nowadays, many of known forest succession simulators follow in modelling these operational levels (Mailly et al., 2000).

One of the most important questions in using the succession models is their credibility. The validation of these models is challenging, because the phenomena they predict takes years or even hundreds of years to follow in nature. Here, the modelled long-term predictions in comparison of undisturbed dataserries of forest dynamics are most valued. The cost of permanent observations is high (the investment must be made yearly over a long time period). Therefore the data of long-term measurements is scarce.

2.4. The basic concept of natural disturbances

The concept of *disturbance* was not used in the older literature, although the dynamic nature of forests was acknowledged from the very beginning (**Paper I**).

The classic definition of *disturbance* is given by Pickett & White (1985): “A disturbance is any relatively discrete event in time (can be seen as a

catastrophe on micro – or macro level) that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.”

In the forestry literature very often the disturbance agent (like *windstorm*) is confused with the disturbance effect - damage caused by the agent (*blowdown*) (Stanturf, 2004). Since the effect of different disturbance agents is different, it is important to distinguish between them.

In general *abiotic disturbances* are of climatic or meteorological origin. Included are wind-related phenomena like: windstorms, tornadoes, hurricanes and typhoons, dust-, snow- and ice storms (Peterson, 2000; Stanturf et al., 2007). Natural fire is one of the most important stand-replacing disturbance agents in boreal and hemiboreal zone. Other climate-related agents like frost and drought can exert a relatively high stress effect on forest ecosystems.

Among the abiotic disturbance agents the *geologic disturbance agents* such as volcanoes, floods, and different kind of mass movements (like snow avalanches and landslides) can be distinguished by their destructive effect to site properties. Here are also included different soil erosion, transport and deposition events (Stanturf, 2004).

Biotic disturbance agents include insects and diseases, invasive plants, and mammalian herbivores (Sousa, 1984).

A causal agent of disturbance has both temporal and spatial dimensions, which are described with: *intensity*, *scale*, *severity* and *frequency* (Stanturf, 2004). *Disturbance intensity* describes the strength of disturbing force by released energy. *Disturbance scale* describes the areal extent of the disturbed area. *Disturbance frequency* is the number of disturbance events per unit time (Sousa, 1984). The *disturbance severity* describes the effect (such as mortality) caused by the disturbance and together with *intensity* they are *disturbance magnitude*.

In forest ecosystems disturbances often create open or altered areas or gaps (Pickett & White, 1985) which spatial and temporal pattern forms a *disturbance regime*. The *disturbance regime* at any site depends on diversity of local disturbance events (Sousa, 1984), their distribution and frequency,

magnitude and the size of the disturbed area, and cannot be predicted from any other large-scale information.

A complex understanding of the disturbance effects on different ecosystem levels is important. In Table 1 the effect of different disturbance agents on three different spatial ecosystem levels are described.

Table 1. Disturbance types altering forest dynamics in boreal and hemiboreal regions. Adapted from Ulanova (2000) and Quine et al. (1999).

Category	Disturbance			
	Single tree	Forest ecosystem	Landscape	
Abiotic	windstorm	stem breakage, uprooting	catastrophic winthrow	
	snow- and ice storm	top and stem breakage	extensive stem breakage	
	tornado, hurricane	abrasion, braking, uprooting	catastrophic multiple damage	
	crown fire	single tree death	catastrophic tree death	
	ground fire	growth reduction, tree death	catastrophic multiple damage	
	drought	tree stress, growth reduction, death	catastrophic tree death	
	frost	tree stress, growth reduction, death	catastrophic tree death	
	volcanoes	single tree death, microsite destruction, growth reduction	catastrophic tree death, site destruction	
	flood	tree stress and death	extensive tree death, site destruction	
	avalanche	single tree death, microsite destruction	catastrophic tree death and site destruction	
Geologic	landslide	single tree death, microsite destruction	catastrophic tree death, site destruction	
	insect	tree stress, growth reduction, death	catastrophic tree death	
	pathogens	tree stress, growth reduction, death	catastrophic tree death	
	invasive species	tree stress	ir-recoverable composition and structure changes	
	herbivores	browsing, debarking, young tree death	extensive browsing, debarking, species exclusion	
	Biotic	insect	tree stress, growth reduction, death	catastrophic tree death
		pathogens	tree stress, growth reduction, death	catastrophic tree death
		invasive species	tree stress	ir-recoverable composition and structure changes
		herbivores	browsing, debarking, young tree death	extensive browsing, debarking, species exclusion
		insect	tree stress, growth reduction, death	catastrophic tree death
pathogens		tree stress, growth reduction, death	catastrophic tree death	
invasive species		tree stress	ir-recoverable composition and structure changes	
herbivores		browsing, debarking, young tree death	extensive browsing, debarking, species exclusion	
insect		tree stress, growth reduction, death	catastrophic tree death	
pathogens		tree stress, growth reduction, death	catastrophic tree death	

2.5. Disturbance agents affecting long-term forest dynamics

Wind has been demonstrated as a crucial factor shaping the structure and dynamics of the boreal forest (Ulanova, 2000; Peterson, 2000; Gromtsev, 2002). Wind creates a complex pattern of damage at a range from individual tree and stand to landscape. The responses of trees to wind-forced swaying, twisting and rocking are bending (abraded and stripped branches and crowns (Hadley & Smith, 1986)), breaking (top or stem breakage) and tipping (partial or full uprooting) (Stanturf et al., 2007). Depending on wind intensity Skvortsova et al. (1983) showed that in European continental boreal forests winds with velocity of 20-25 m/sec have catastrophic effects (extensive windthrow or uprooting). The gap size formed after low- or moderate-severity windthrows varies from 100 to 10,000 m² (Skvortsova et al., 1983).

Fire has long been acknowledged as a crucial factor shaping boreal forest structure and development (Sirén, 1955; Johnson, 1992; Niklasson & Granström, 2000). There is wide variability in fire behaviour and regimes in boreal and hemiboreal regions, still roughly fires range from infrequent high-severity stand-replacing fires to frequent low-severity surface fires (Oliver & Larson, 1996). The 'natural' fire regimes vary in different parts of the boreal forest (Weir et al., 2000; Gromtsev, 2002; Ryan, 2002). It has been estimated that the mean frequency of fires in Russia's European boreal forests vary from 1-2 per century to 1-2 per millennium (Gromtsev, 2002). The studies in Sweden indicate that until 150 years ago the natural fire cycle varied between 50 and 100 years (Zackrisson, 1977; Niklasson & Granström, 2000), with the shortest period of 20 years in average (Wallenius et al., 2007). In the North American boreal forest the natural fire cycle ranges from an average 50 to 200 (500) years (Bonan & Shugart, 1989). The human impact on fire regimes also differ. Depending on the region, 3 - 70% of fires in boreal Eurasia are natural fires, i.e. ignited by lightning (Gromtsev, 2002).

Insect and disease outbreaks annually alter yearly large areas in Northern American boreal forests (Logan et al., 2003; Berg et al., 2006), whereas in pristine and seminatural European boreal forests they do not cause large-scale disturbances (**Paper I**). In general in forest ecosystems insects and pathogens remain at the particular site or in neighbouring stands at low occurrence. The epidemic or stand replacing disturbance level can be achieved, when trees become weakened by other factors (other

disturbances, climate change). Weakened trees are less resistant to the insect and disease attacks, allowing them build up populations and reach the level where they are able to kill also vigorous trees (Oliver & Larson, 1996; Berg et al., 2006). Still as 'internal' or chronic disturbance agents they cause formation of gaps (Morozov, 1925; Voropanov, 1950). In contrast, biotic disturbances play an important role in Siberia, often 'substituting' for windthrow (Selikhovkin, 2005) as a disturbance agent in late-successional stands. For example, in the Irkutsk region during the period 1870-1963 app. 1,061 million ha of Siberian pine forests died due to attack by the Siberian silk moth *Dendrolimus sibiricus superans* Tschetv. During the last 40 years outbreaks of this pest were registered in the area of 1,465,000 ha (Vaschuk & Shvidenko, 2006). The main host of this insect is Siberian pine and, to a lesser extent, larch, fir, spruce and pine. The impact of these outbreaks is most severe when followed by fires (Furyaev, 1970), because of high fuel loads of standing dead wood (Verkhunov, 1970). Other insects able to cause significant forest dieback include dingy larch bell (*Zeiraphera diniana* Gn.), saddleback looper (*Ectropis crepuscularia* Denis & Schiffermüller), as well as secondary pests: six-toothed bark beetle (*Ips sexdentatus* Boern.), eight-toothed bark beetle (*I. acuminatus* Gyllen.), pine shoot beetle (*Tomicus piniperda* L.), lesser pine shoot beetle (*Tomicus minor* Hart.), longhorn beetle (*Spondylis buprestoides* L.), great spruce bark beetle (*Dendroctonus micans* Kugel.) and Pissodes weevil (*Pissodes piniphilus* Herbst.) (Prozorov, 1929).

Wild *mammalian herbivores* have played and still have an important role in shaping the boreal and hemiboreal forests (Oliver & Larson, 1996; Pucek, 2004). The long-term effect to forest ecosystem structure comes from recurrent grazing and browsing (Kraśńska & Kraśński, 2007; de Chantal & Granström, 2007) but also breaking smaller stems and debarking larger trees (Oliver & Larson, 1996). The most common species in Fennoscandia are moose (*Alces alces* L.), roe deer (*Capreolus capreolus* L.) and hare (*Lepus europaeus* Pallas.), in Northern America elk (*Cervus canadensis* Ex.) (Oliver & Larson, 1996). The mostly absent effect of previously/historically important great grazers, buffalo (*Bison bison* H.) Northern America (Oliver & Larson, 1996) and European bison (*Bison bonasus* L.) in Eurasia (Pucek, 2004; Kraśńska & Kraśński, 2007), has been resumed with the introduction of domestic livestock.

2.6. Field experiments for studying long-term forest dynamics

In forest research field experiments may be distinguished according to their basic design and time scale. Examples of field experiments of specific design are 1) manipulated experiments, where based on a set of predefined treatments the ecosystems responses to these treatments are compared and tested with the hypothesis (Cox, 1958), and 2) comparative observational studies, where the actual status of a population is assessed without actively pre-defining or changing the site conditions (Kuehl, 1994).

In studying long-term responses of forest ecosystems the observational time scale becomes important. Based on the time scale, it is possible to distinguish three types of trials which may provide data for long-term dynamics. Longitudinal studies (“permanent trials”) are established and re-measured, usually at regular intervals over long periods of time. The idea is to capture the development over the whole lifespan of ecosystem successional cycles and an important advantage is the ability to reconstruct the life history of one particular tree or a population of trees for a given set of influencing variables within the successional phase of interest. The biggest disadvantages are the long wait for data and high investment capacity over the time. Due to these constraints the objective of the trial may not always be achieved, since plots may be destroyed or abandoned prematurely due to changing environmental conditions or research policies (**Paper III**).

Chronosequences provide a quick solution in a research situation where no information is available about population development. They generally are measured only once, but they need to cover the entire range of ages and growing sites. The sequence of re-measurements in time is substituted by simultaneous point measurements in space assuming “normal” effect of natural or human-induced disturbances (Wenk et al., 1990). The biggest constraint in using the temporary plots for dynamics studies is the fact that these point descriptions do not provide information about change rates of the target variables. Therefore, most of the contemporary modelling techniques cannot be applied (Gadow & Hui, 1999).

Interval studies (in forestry literature also known as “cross-sectional studies”) provide a compromise way between the two contrasting approaches described above. Interval plots are measured at least twice and spread over a range of growing sites, successional development stages and land use or management categories. They combine the advantages of the

permanent plot and the temporary plots by describing the change rates of studied variables with minimum wait for data (Gadow & Hui, 1999). The only constraint is that the interval between two successive measurements is needed to be sufficiently long for including the short-term effects of climatic or seasonal variability.

In successional studies the long-term experiments can be well exploited in explaining the mechanisms of ecosystem change in between and within different stages of system development. More important is the fact that the same permanent plot information, depending of course on study design, can be used in describing the same phenomena at different spatial levels of forest ecosystem. The investigation results in single and small-scale dynamics can be generalized to population or landscape level. Generalizability depends on whether or not the observed response measurement is representative. It must be clear that the study sites are representatively sampled and if the results of the observations may be legitimately extended to the general population of conditions to which the research findings need to be extended (Gadow & Kleinn, 2005).

2.7. Research needs

The Intergovernmental Panel of Climate Change made an assessment of climate change related long-term and large scale trends to the observed causal changes in biological systems (McCarthy et al., 2001). Their stated changes in general biological trends confirm the fact that changed climate is already affecting current living natural systems (Parmesan & Yohe, 2003).

The changes in regional or global biological diversity reflect the reactions of organisms in these ecological systems to modified environment conditions. In a global context, sometimes the biologists or economists do not see that “the forests are for the trees” and their responses and development can not be understood without knowledge of the trees and related species (Hansen et al., 2001). The changes in the behaviour of any single species, taxon or geographic region have a number of possible explanations (Parmesan & Yohe, 2003) including not only climate change but also globally extensive human-induced land-use changes. The forest trees are in this respect long-living organism and therefore forest ecosystems need to adapt to changing environmental conditions and escalating societal demands (Dobbertin, 2009). For evaluating risks in forests and forestry linked to climate and

human-induced changes into disturbance regimes a continuous disturbance monitoring and assessment is needed. The understanding of the effect of disturbance agents acting at different spatial scales enables more precise effect modelling and large scale forest development simulation for supporting economically and ecologically balanced management decisions in future. Thus the functional aspects enable modelling for decision-making.

The information and knowledge about forest dynamics processes and resulting landscape patterns have been collected in piecemeal fashion over long time periods. Together with improved understanding in forest dynamics the concept of sustainable use of forest resources has developed. The common understanding of forest management has been developing together with the knowledge of human impact to forest systems and broadening ways for forest utilization. The concept of ecosystem management and other sustainable forest management planning principles suggest that currently but even more so in the future forest management activities need to follow or mimic natural processes driving forest ecosystems development (**Paper II**). In ecology and ecologically informed management planning, acceptance of non-equilibrium states of ecosystems and the important role of disturbances and its characteristics in shaping the processes have been acknowledged (Turner et al., 2003). Still, for the emulation of natural disturbance regimes into ecologically sound forest management planning, more profound and complex information is needed in the changing effect of disturbance characteristics (Kimmins, 2004).

The high number of studies made on disturbance effects in various biomes and on different spatial and temporal levels provides a good base for management design and decision support. Still there is a gap in knowledge of how different disturbances affect and co-act between different spatial levels and what would be the best factors for describing these interactions.

3. AIMS OF THE STUDY

Understanding effects of disturbances on boreal and hemiboreal forest structure and dynamics is greatly needed. The changes in climate may be followed by changes in natural disturbance regimes and these will have effect to forest structure, species composition and ecological processes (Nilson et al., 1999). On the other hand, increasing and changing anthropogenic impact is reflected as continuous reorganization of forested landscapes. In classic forest management, usually a harvest event follows after a major natural disturbance.

This thesis incorporates current theoretical and practical knowledge on natural and anthropogenic disturbance dynamics in boreal and hemiboreal zone as well as integrates it into adaptive forest management and planning methods.

The aims of the present doctoral thesis are:

1. To understand interactions between different variables characterizing disturbance mechanisms and to match new approaches with classical experience (**Paper I and II**);
2. To create a long-term forest successional development scheme where the basic management actions, in stands with different initial conditions and environmental conditions, match with natural development (**Paper II**);
3. To verify the hypothesis that variation of tree mortality is high and even old stands can demonstrate high NEP due to low mortality rates (**Paper II and III**).
4. To determine and test basic variables or their combinations for creating realistic model runs that describe the long-term stand dynamics (**Paper IV and V**).
5. To create the methodology for calculating mean height in juvenile stands, which corresponds to classical mean height in mature stands.

4. MATERIAL AND METHODS

4.1. Permanent forest experiment observations

Three different sets of permanent sample plots have been used in the studies of the current thesis.

4.1.1. Long-term field experiments at Järvelja

The history of empirical forest research in Estonia can be traced back to 19th century. The establishment of well-designed and documented field experiments for forest research purposes began after the establishment of the Järvelja Forestry Training and Research Centre in 1921 (Mathiesen & Riisberg, 1932). The Järvelja experimental forest is located in the South-Eastern region of Estonia near Lake Peipsi (at 58°16'N, 27°18'E).

Among the early long-term forest experimental series in Järvelja are growth and yield experiments initiated in 1921 by Andres Mathiesen (Kasesalu, 2003) and thinning experiments initiated by August Karu and Lembit Muiste (Tullus & Reisner, 1998). All together, 115 long-term forest growth and yield monitoring plots were established during the period 1922 to 1935. The rectangular experimental plots were relatively small covering between 400 and 600 m². The small plot size was aimed to compensate with a high number of replicates within the same stand, but in reality the variation of plot characteristics was too large. The experimental sites were selected so that all forest sites and dominant tree species in the Järvelja region were represented. The basic stand variables were measured (dbh distributions, random tree heights) and trees on the plots were numbered (Paper III).

In the late 1990s it was decided to systematically “revive” these old field plots most of which had been abandoned in 1959. From the 115 previously abandoned plots, it was possible to revive only 65 plots. The distribution of these plots over the different site types and for the different forest types, characterized by the dominant species is presented in Table 2.

Table 2. Research plots (JLTFE) at Järvelja by site types and dominant tree species.

Group of types	Pine	Spruce	Birch	Other	Total
<i>Fully drained swamp forests</i>	5		1		6
<i>Meso-eutrophic forests</i>	6	4	1		11
<i>Mesotrophic forests</i>	22	13	1		36
<i>Nemoral forests</i>		2	2	3	7
<i>Bog moss forests</i>	5				5
Total	38	19	5	3	65

For analyzing the stand development trends in the **Paper II** data from 37 growth and yield permanent sample plots were used. These plots were established from 1925 to 1935. On average there have been 9 measurements for each plot from 1925 to 2004. The average size of plots is 0.12 ha. The Scots pine was the dominant tree species on 30 plots, birch (*Betula pendula* Roth) on 3 plots and Norway spruce (*Picea abies* (L.) Karst.) on 4 plots. The average stand age on the year 2004 on Scots pine dominated plots was 126 years, birch dominated 107 years and Norway spruce dominated 104 years. The stand age varies from 73 up to 203 years on different plots.

For analyzing stand development processes on fresh boreal forest type for stands where Scots pine was dominant tree species, data from 18 permanent sample plots was used.

Regeneration study plots at Järvelja were established in 2005 at exact locations of the previous JLTFE plots (series of nine study areas). This is to study stand regeneration and growth dynamics in young forests in the next forest generation of previously measured experimental areas. Sample areas are placed in three different stands and were located in nine study groups. Sample areas were distributed among stands at even intervals of 50 meters. The sample plots inside the study areas were located using cluster arrangement as described in **Paper V**. Every cluster included five circular 50 m² size plots (radii = 4 m).

The centre of the middle plot in a cluster was set in the centre of a study area. The other four plots were located at exact 10 meters to the north, south, east and west direction from the centre. The plot centre was marked

with a metal pole. Furthermore, all plots were divided into four sectors (each 12.5 m²) following the north-south and west-east axes. Each sector was numbered, starting from the northeast quarter.

Table 3. Stand component data from Järvselja plots.

Tree species	Number of stand components	Tree height, m		Number of trees
		Min	Max	
all	146	0.05	13.90	10086
all conifers	43	0.80	10.90	1819
all broadleaves	103	0.05	13.90	8267
pine	7	0.80	2.87	38
spruce	36	0.80	10.90	1781
birch	36	0.79	12.80	3973
aspen	18	0.41	13.90	2425
linden	15	0.05	7.70	912
other broadleaves	34	0.80	6.80	957

During the first four measurement occasions tree height for all trees taller than 0.8 meters from the ground level were measured. Beginning in 2008 all tree heights were measured starting from the ground level. The tree records at each re-measurement included sector number, tree layer, tree species and total tree height. Within each sample plot sector, the three tallest sample trees were selected from the dominant tree species. In addition, one sample tree was selected for every other tree species found in the sector. For each sample tree higher than 1.3 meters, dbh in two directions (to plot centre direction and perpendicular), total height, the height of living crown base and height of lowest dead branch (thickness ≥ 2 cm, length ≥ 10 cm) were measured. Damage on the sample trees was recorded, classified according to cause and severity. In addition, tree coordinates were assessed from the centre of cluster for all sample trees.

The stands were initially measured in July and August in 2005, and re-measured at the end of the growing season (September, October) in 2006, 2007 and 2008. The four different measurement periods were considered independently in data analysis and included in total 10,086 single tree

measurements distributed between 146 stand components. The general stand component data is presented in Table 3.

4.1.2. The Estonian network of forest growth and yield plots

The Estonian forest research plots network (ENFRP) was established in 1995 and was designed using experience from Finnish studies (Gustavsen et al., 1988) to provide empirical data for developing forest growth and yield models (Kiviste et al., 2003). In 2009, 730 regularly re-measured field plots are distributed randomly in two- to ten-plot clusters over the entire land surface of Estonia, mainly following the grid of ICP Forest level I monitoring plots (Karoles et al., 2000). Most plots are in heath, mesotrophic, meso-eutrophic and nemoral forest site types. The spatial distribution of the plot locations is presented in Figure 2. The data from consecutive measurement with five year intervals were used in the **Paper III, IV and V**.



Figure 2. Geographic location and spatial distribution of the ENFRP plots. Each circle on the map presents a cluster of two to ten sample plots. On the map the circles represent all monitoring areas and the filled dots Scots pine dominated sample plots used in **Paper IV**.

The plots are circular with a varying radius (15, 20, 25 or 30 meters) including at least 100 main storey trees. Second-storey and under-storey trees are measured in an inner circle with a radius of 8 or 10 meters depending on the main plot radius. For all trees on the plot, the tree location coordinates are determined and diameters are measured. In addition, the tree height and crown length is measured for each fifth tree. The age of different stand components is determined by counting tree rings from core samples extracted from sample trees. The re-measurements on the plots are being carried out at five-year interval.

For the stand development modelling in **Paper IV** Scots pine dominated (the proportion of pine volume exceeded 50% of stand volume) plots were selected. 142 five year growth intervals from 134 Scots pine dominated plots were used in conducting growth models.

4.2. Tracking the disturbances in forest experiment data

Irregular measurement intervals in forest growth studies are quite common. They often occur when previously abandoned field plots are “revived”, i.e. re-measured after long periods of time during which no observations are available. When analysing disturbances for irregular measurement intervals, the observed time interval between re-measurements does not match the desired modelling interval. Thus, modelling annual tree growth and survival based on data with irregular measurement intervals requires specific interpolation of the independent variables during such “measurement gaps”, as demonstrated by Nord-Larsen (2006).

4.2.1. Irregularities in measurements

Originally, re-measurement intervals in the experimental areas were planned to range between five to ten years. However, because these areas were used in forestry students’ field training; they were re-measured more frequently during first decade after establishment. The measurement data were stored in handwritten data journals and experimental case files. The last of these handwritten records dates back to 1959. Some of the plots were re-measured in 1977, 1984, and 1995, but for the majority of the growth and yield plots, no measurements were done between 1959 and 2004 (**Paper III**).

When analyzing and exploiting old data series like the one described above, we must be aware of possible constraints induced by uncertainties and inconsistencies in measuring and data recording. These inconsistencies can be classified according to the following categories (**Paper III**):

- 1) *Changes in experimental design and measurement prescription.* During long period of observation, governmental policies and general research funding principles may change, which can have severe effects on financing ongoing long-term study projects. Such changes may cause the termination of existing field experiments. Old experimental designs cannot meet the demands of new research objectives and this will result in modifications of measurement prescriptions. In Järvelja during the early years, the main focus was on compiling stand diameter distributions. Only few tree heights were measured. However, soon a demand for yield tables had to be satisfied, requiring tree heights for volume calculations. Later on, tree mapping was introduced for the study of spatial forest structure requiring known tree positions.
- 2) *High variability in measurement staff and assessment techniques.* Over long measurement periods different people are responsible for carrying out the fieldwork. The measurement accuracy within series of consecutive re-measurements may vary substantially due to changing staff. Also, during the course of extended observation periods different measuring devices are used. In the first measurement years tree heights were often measured using a theodolite. At the same time the heights of all the removed trees (representing the suppressed part of the plot) were measured with a measuring tape. The result of this separation was two different height-diameter relations.
- 3) *Changes in data recording and storing.* The biggest change in data recording was the transfer of the old handwritten experimental case files to digital data recording. During data conversion and digitizing it is possible to generate errors due to typing and misinterpretation of certain remarks in the old books. Special care was taken in the digitizing of the Järvelja experimental data. Outliers especially were double checked (Hordo, 2004; 2005). Nevertheless, some uncertainties still remain.

4.2.2. Tracking the disturbances

On the data of the JLTFE study plots is possible to distinguish between the trees which were found dead at the end of a particular measurement interval and between the trees removed over a thinning operation during the measurement interval.

In Estonia forest management activities are recorded in forest management plans, which provide an opportunity to recover some disturbance events. Plot M046_11_01 is a typical example of a research plot which had been measured during irregular time intervals between 1926 and 2008. The shortest interval between two successive measurements was one year. During the gap period, only sanitary cuttings were carried out in the stand, in 1974, 1976, 1977, 1980, 1996 and 1999. These cuttings removed only dead trees, but we do not know when these trees had died and how many had died in a particular year. We also have no knowledge about the dimensions of the dead trees during the gap period. We know the number of trees that were recorded missing during the gap interval. We also know that the removed trees were not alive when cut.

For every re-measurement we calculated the accumulated number of trees cut and dead $cNx_t = \sum_{i=1}^t Nx_i$, where cNx_t refers to the accumulated number of trees separately for each cut (x=cut) and dead (x=dead) trees at the enumeration period t, Nx_i is number of trees at the enumeration period i, t is measurement interval (years). The number of unknown trees for a particular tree species is obtained from the initial total number of trees of that species minus the cut, recorded dead and live trees. For this plot no measurements are available between 1959 and 2004. Re-measurements started again in 2004, after a “gap” of 45 years. Relevant details about the available natural and anthropogenic disturbances are listed in Table 4.

The weight of a registered disturbance can be described by the ratio between removed and total basal area and be designated by using the symbol rG. The preference of a disturbance refers to the relative tree size removed from the population. Murray & Gadow (1991) used the difference between the mean diameters of the removed and the remaining trees, divided by the diameter standard deviation of the whole stand to describe the type of thinning. In this study the so-called NG ratio is used and defined as follows:

$$NG = \frac{rN}{rG} = \frac{N_{thn} / N_{tot}}{G_{thn} / G_{tot}} \quad (1)$$

where N_{thn} and N_{tot} are removed and total number of trees; G_{thn} , G_{tot} are removed and total basal area.

Table 4. Details about the natural and anthropogenic disturbances in the research plot M046_11_01.

Year	Area (ha)	Number of trees per ha			Basal area m ² per ha			Cumul. trees per ha				
		live	cut	dead	live	cut	dead	rG	NG	unknown	cut	dead
1	2	3	4	5	5	7	8	9	10	11	12	13
1926	0.06	2617			35.65			0.00	0.00			
1929	0.06	2433		183	36.97		1.54	0.04	1.75	1		183
1930	0.06	2333		100	37.54		1.21	0.03	1.32	1		283
1931	0.06	2250		33	37.22		0.22	0.01	2.46	51		316
1932	0.06	2183		67	37.33		0.50	0.01	2.25	51		383
1933	0.06	1600	500	83	32.70	4.56	0.78	0.14	1.90	51	500	466
1934	0.06	1517	67		32.48	0.99		0.03	1.43	67	567	466
1938	0.06	1467	50		35.14	0.36		0.01	3.25	67	617	466
1942	0.06		433				6.87	0.00	0.00			1050
1948	0.06	767			30.13			0.00	0.00	1050	1050	466
1951	0.06	650	117		28.24	3.27		0.10	1.47	1167	1167	466
1959	0.06	483	67	17	25.47	2.19	0.36	0.09	1.63	1234	1234	483
2004	0.06	217			25.13			0.00	0.00	1234	1234	483
2008	0.06	217			27.92			0.00	0.00	1234	1234	483

The values for rG and NG for the different measurement years are shown in columns 9 and 10 of Table 4. Evidently, the thinnings were usually weak to moderate, ranging from 1 to 14 percent of basal area removed. The NG-ratio varied between 1.32 and 3.25, indicating also very low thinnings.

We also traced disturbance events for an experiment involving a mixed forest with two tree species. The two tree species are *Betula pendula* (Roth.) and *Pinus sylvestris* (L.).

Table 5 presents relevant details of the plot with two species. The number of birch trees was reduced to about one half of the original number during

the 79-year observation period. The number of pine trees decreased from 1600 per ha in 1925 to 283 per ha in 2004. Only 17 percent of the pine community was at the site in the end of observation period.

The basal areas of the two species has been increasing due to tree growth and decreasing due to mortality and pre-emptive removal of some small trees that were still alive but were expected to die in the immediate future. Therefore, the values of rG and NG can only be evaluated during a particular harvest event, i.e. if we can identify the trees which were leaving the community during a specific measurement interval.

Table 5. Details about the natural and anthropogenic disturbances in the research plot M274_04_02.

Year	Area (ha)	Species	Number of trees (per ha)		Basal area (m ² per ha)			rG	NG	Cumul. trees per ha			
			live	cut	dead	live	cut			dead	unknown	cut	dead
1	2	3	4	5	5	7	8	9	10	11	12	13	14
1925	0.06	Birch	67			2.23			0.000	0.000			
1925	0.06	Pine	1600			28.47			0.000	0.000			
1926	0.06	Birch	67			2.29			0.000	0.000			
1926	0.06	Pine	1517			29.04			0.000	0.000	83		
1928	0.06	Birch	67			2.54			0.000	0.000			
1928	0.06	Pine	1267			28.47			0.000	0.000	333		
1929	0.06	Birch	67			2.56			0.000	0.000			
1929	0.06	Pine	1200	67		28.34		0.57	0.020	2.658	333		67
1930	0.06	Birch	67			2.56			0.000	0.000			
1930	0.06	Pine	1200			28.34			0.000	0.000	333		67
1931	0.06	Birch	67			2.68			0.000	0.000			
1931	0.06	Pine	1100	50		28.10		0.53	0.018	2.364	383		117
1932	0.06	Birch	50			2.54			0.000	0.000	17		
1932	0.06	Pine	1050	17		27.63		0.24	0.009	1.799	417		133
1933	0.06	Birch	50			2.61			0.000	0.000	17		
1933	0.06	Pine	683	350	17	22.67	5.48	0.08	0.197	1.773	417	350	150
1935	0.06	Birch	50			2.65			0.000	0.000	17		
1935	0.06	Pine	650			22.57			0.000	0.000	450	350	150
1937	0.06	Birch	50			2.71			0.000	0.000	17		
1937	0.06	Pine	583	67		22.96	1.35		0.056	1.842	450	417	150
1941	0.06	Birch	50			2.90			0.000	0.000	17		
1941	0.06	Pine	567			23.00			0.000	0.000	467	417	150
1948	0.06	Birch	50			3.13			0.000	0.000	17		
1948	0.06	Pine	433	17		20.61	1.19		0.055	0.676	583	434	150
1995	0.06	Birch	33			4.58			0.000	0.000	33		
1995	0.06	Pine	267			33.19			0.000	0.000	750	434	150
2004	0.06	Birch	33			4.11			0.000	0.000	33		
2004	0.06	Pine	283			36.47			0.000	0.000	733	434	150

5. RESULTS

5.1. Conceptual model of stand development

In this thesis (**Paper II**) the four basic stages described by Frelich (2002) were modified (Figure 3) to fit the theoretical development trend of tree stands on a fresh boreal forest type after a stand replacing disturbance.

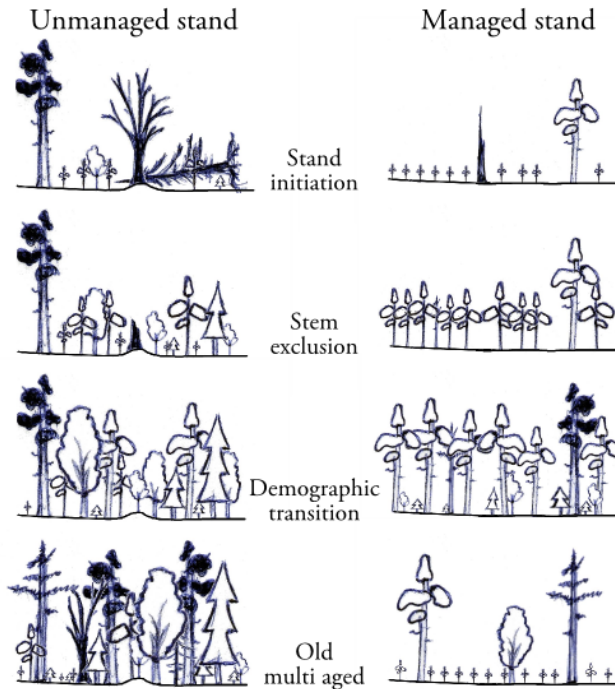


Figure 3. Successional developments of forest stand on fresh boreal forest type.

The effect of intensive management on the forest stand structure and composition produces a marked distinction between unmanaged and managed stands (Rouvinen & Kuuluvainen, 2005; Kangur et al., 2004; Kuuluvainen et al., 2002).

The stand initiation stage (1) follows a major disturbance. This disturbance can be natural (stand-levelling storm, crown fire, insect or fungi attack) or anthropogenic (clear-cut logging). This initiation stage lasts from the stand replacing disturbance until the continuous canopy forms and trees begin competing with each other for light and canopy space. During the stem exclusion stage (2) the canopy is dense enough to prevent new

saplings from growing into the canopy. The stem exclusion stage lasts until the tree canopy is dense enough to induce a density dependent ‘self-thinning’ mortality in the stand. The demographic transition phase (3) is characterized by a heterogeneous stand structure with, in particular, an irregular spacing (Kuuluvainen, 2002). The under-storey establishment in this stage is an essential component for the shift to an old, multi-aged stand. During the old multi aged phase (4) the under-storey formation is a characteristic, site specific process (Jögiste & Väät, 2002). Following the general management planning principles, the managed stands will reach to the end of economically feasible rotation period before the shift to an old, multi aged stage.

5.2. Reconstruction of disturbances

Figure 4 shows a typical example of a research plot that has been measured at irregular time intervals between 1926 and 2008. The shortest interval between two successive measurements was one year. The longest interval, denominated by the “gap” in Figure 4, where data are not available during the period between 1959 and 2004, was 45 years. The measurement years are indicated by black spots just below the x-axis. The graph on above on Figure 4 presents the quartile lines of the diameter distribution and thus shows how the forest structure has changed during the last 82 years. The development of a single tree diameter is shown in Figure 4 in relation with the diameter distribution of the plot. A pine tree (dash and dot line) which in 1895 had reached breast height (1.3 m) was cut in 2006 for stem analysis to recover the complete history of diameter and height growth. In 1920, the tree belonged to the 75 % quartile of the diameter distribution. In 2006 it was in the 25% quartile of the diameter distribution.

The graph on bottom of Figure 4 shows the development of the live trees and the accumulated number of outgoing trees per ha during the 82-year observation period. At every enumeration all trees were measured, including the dead ones, so the size distribution refers to all trees. When trying to analyse dead trees for the entire 82-year period, during the gap period, only the number of dead trees is known, not their size distribution. Therefore, it is important to distinguish between the dead trees that were recorded before 1960 and since 2004, and those that died during the gap period.

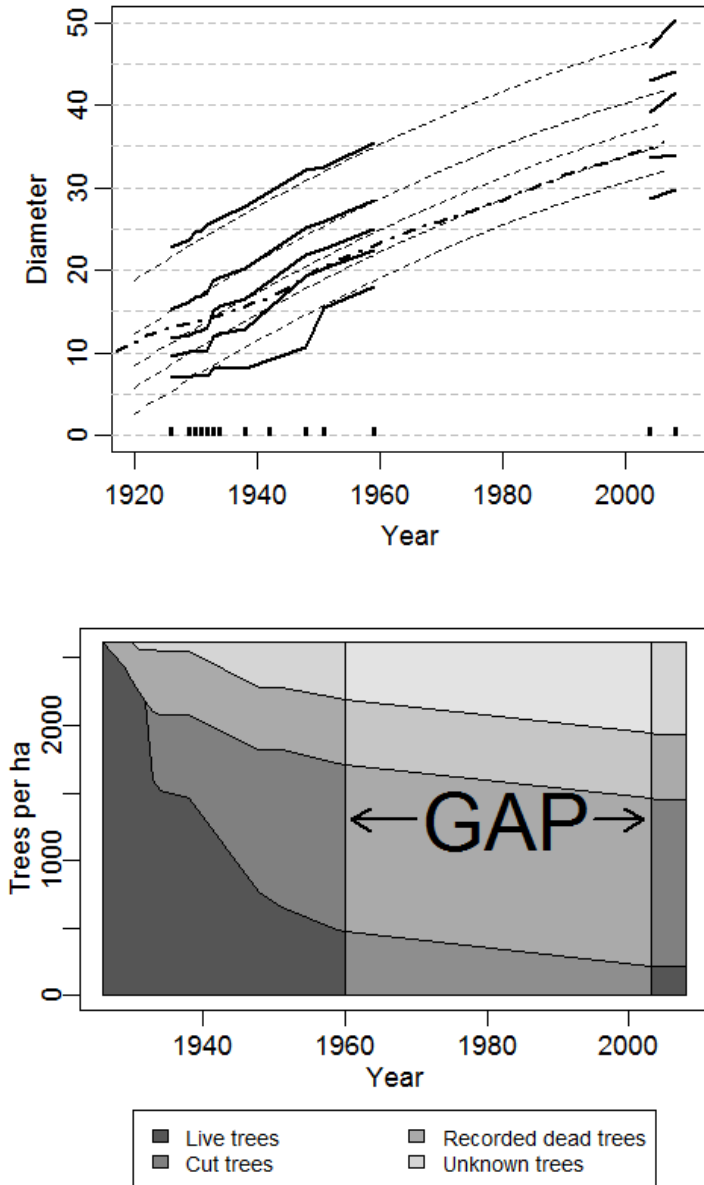


Figure 4. Empirical (solid lines) and predicted/smoothed (dashed lines) quartiles of diameter distribution (upwards 0, 25, 50, 75 and 100) over time for the research plot M046_11_01 (above). The stem analysis for one pine tree is presented as a dash-dot line. The plot had been measured during irregular time intervals between 1926 and 1959, and again in 2004 and 2008 (black spots at the bottom line; the measurement years are shown in Table 4). The developments of live and cumulative outgoing trees are shown in the graph on below.

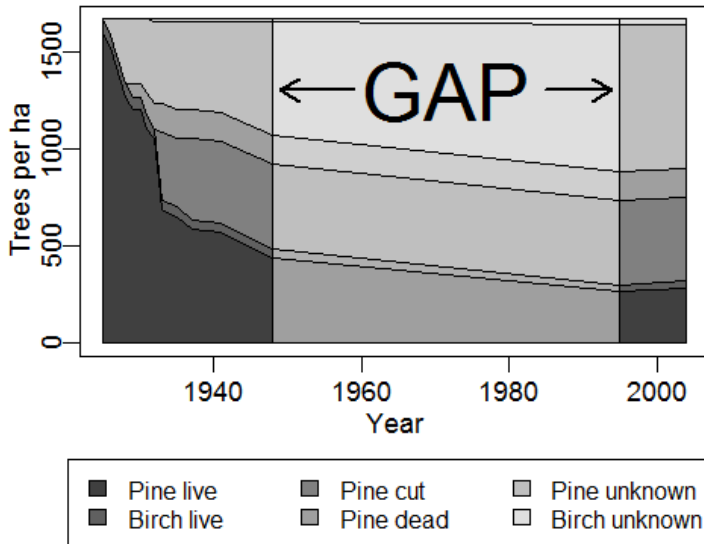
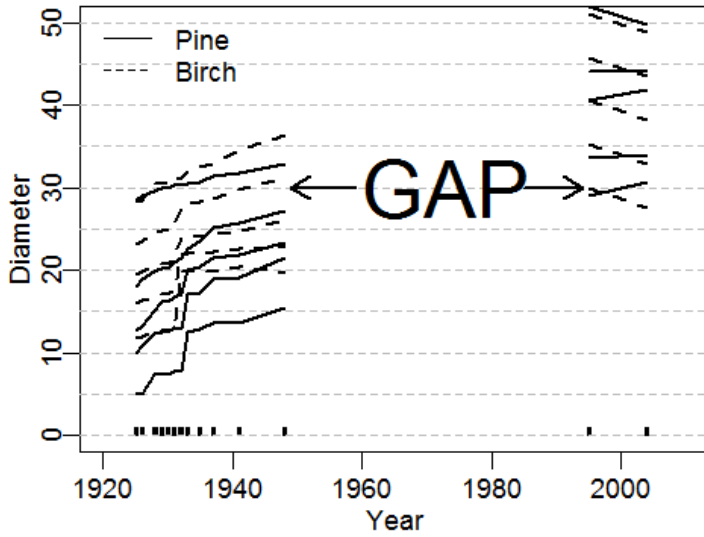


Figure 5. Development of the four quartiles (upwards 0, 25, 50, 75 and 100) of the diameter distribution (above graph) of pine and birch community on the research plot M274_04_02 and development of outgoing trees (below graph). The plot had been measured (spots at bottom) during irregular time intervals between 1926 and 1959, and again in 2004 and 2008.

Disturbance occurrence was also recovered for an experiment involving a mixed forest community with two tree species. Figure 5 presents stand development trends of pine and birch mixed stand similarly to corresponding graphs from pure pine plot data presented on Figure 4.

The graph shows that initially the birch was dominant, which is quite common in a Pine/Birch community. The dominance of Birch has disappeared, and both tree species distributions look quite similar after 79 years of observation.

5.3. Long-term prediction of stand development

We can only predict growth and survival if the interval is a period of undisturbed growth. However, to evaluate different management scenarios, we must be able to model the disturbance events as well as the growth. A basic assumption with interval plots is that the interval is a period of undisturbed growth. All models in this study, except the Kiviste difference equations (Kiviste, 1999a; 1999b), were developed or calibrated on the undisturbed interval plot data. The growth models include natural growth and natural single tree survival but they do not include anthropogenic interference as can be expected in the case of commercial forests. These models therefore allow us to predict stand growth in commercial forests between harvest events in the long run.

“Est” simulation models have been developed on the basis of forest inventory data, which contain both natural mortality (gap phase disturbances) and thinnings and can be used for long-term prediction. The use of growth models developed on interval plot data in long-term prediction necessitates including both natural and anthropogenic disturbances. An example of the long-term prediction of stand basal area and volume development simulated with the “D.G” simulation combination in comparison with “Est”, which represents the average development of Estonian stands, appears in Figure 6. In the “D.G” model combination (Table 2 in **Paper IV**), calculations were repeated with five-year intervals up to 120 years, and the degree of stocking was calculated for every step with the Eq. 15 in **Paper IV**. When the degree of stocking exceeded a value of 90%, the basal area and number of trees was then reduced by 30%, following the Estonian thinning instructions. In spite of different performance in short-term prediction, both simulation combinations showed quite comparable performance in long-term projections.

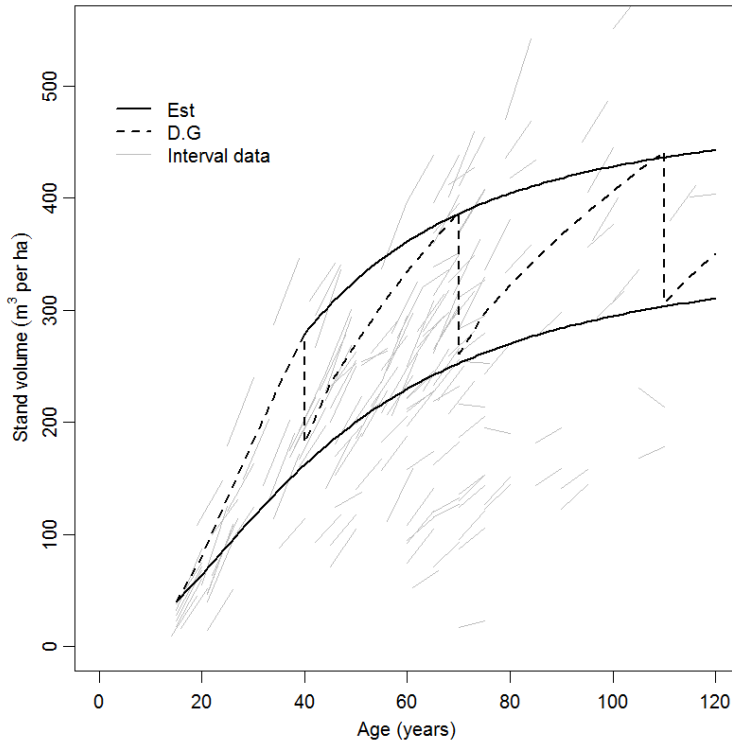


Figure 6. An example of long-term prediction with the “Est” and “D.G.” simulations. The initial data from one sample plot was used ($A = 15$ years, $D = 5.6$ cm, $H = 5.4$ m, $G = 13.0$ m² per ha, $V = 40$ m³ per ha).

The main advantage of the use of algebraic difference equations over the fixed-step increment equations is the ability to use flexible time steps. However, experience has shown that the projection intervals should not deviate too much from the time steps of the measurement data. An important constraint when using the algebraic difference equations is to avoid long-term predictions in one prediction sequence.

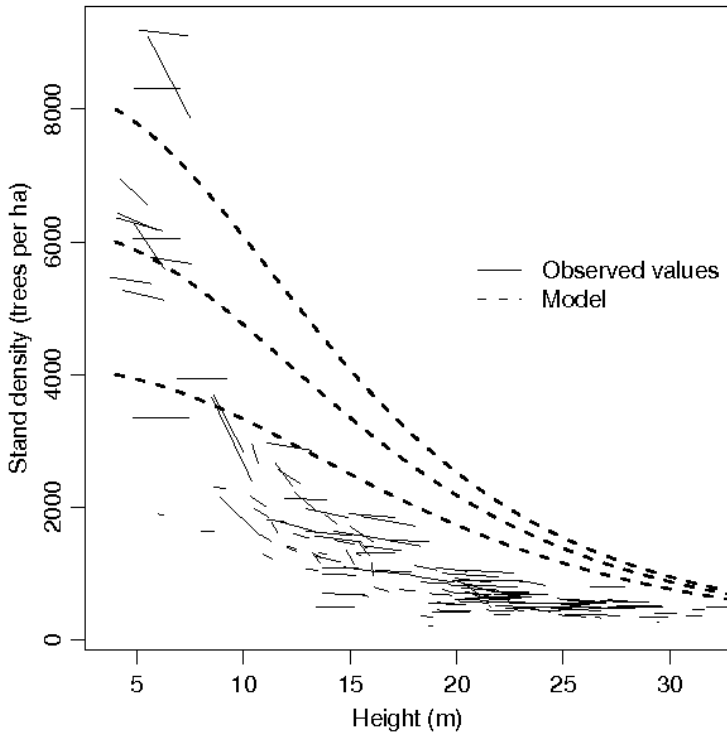


Figure 7. The algebraic difference models prediction trajectories with three different initial states in comparison with the observed data from the Estonian network of permanent forest growth and yield monitoring plots.

Figure 7 shows an example of the long-term projection of stand density in three different initial densities. A remarkable variance in model predictions in comparison of observed values can be seen. This typically happens when only non-overlapping intervals have been used in the model parameter estimation. It is often advisable to use all possible intervals, but even in that case one has to be careful with long-term projections in one sequence.

6. DISCUSSION

6.1. Long-term field plot data for forest dynamics studies

Pickett et al. (1987) distinguish between pathways, causes and mechanisms of vegetation change in order to explain the dynamics of succession. They define a pathway as a temporal pattern of vegetation change and a cause as an agent, circumstance or action responsible for successional patterns. Permanent field plots can provide observations about pathways of succession, but may also generate hypotheses on mechanisms and causes. This is especially relevant if the communities are protected from human interference, but is also valid in managed forests where the objective is to explain particular response patterns following specific harvesting operations.

The permanent plot observations enabled the description of both external and internal causes and mechanisms of stand dynamics. When considering the causes of succession it is necessary to distinguish between the immediate and long-term causes. In different stand development phases the importance of different factors directing the processes can change (Bakker et al., 1996). In a stand initiation the site properties and the competition with competing vegetation are more important than in the stem exclusion phase (Frelich, 2002), where the self competition mechanisms for light and nutrient availability start to prevail (**Paper II**).

Analysis of forest stand development on the JLTFE plots indicate that there is still a considerable volume increase in stands that are over 100 years old and the net ecosystem productivity is at considerable level in these old stands (Peet, 1992). The gradual increase in volume exceeds considerably the Kiviste (1999 a; b) model's average prediction. This suggests that the net ecosystem productivity can be high in old stands. The total productivity can be only slightly higher, because the intermediate cuttings have been mild (**Paper II**). The Scots pine dominated JLTFE study plots are mainly in two age groups: stands less than 100 and stands between 100 and 200 years old. On observed sample plots surprisingly high stand density can be detected during the whole study period. In both time series groups there has been a noticeable stand density increase during the last decades. At the same time, stand mean diameter values have been declining. These two phenomena can be related to two different aspects in stand development. Stands in the younger time series group undergo a development of a stem

exclusion stage and reach the phase of demographic transition and stands in an older time series group undergo a development of a demographic transition stage and reach to the phase of old multi-age forest (Frelich, 2002). Here we can conclude the relatively modest external disturbance influence and allogenic change mechanism of stands.

The establishment and maintenance of a series of permanent plots requires a firm commitment beyond short-term economic fluctuations and political changes. Nevertheless, it may happen that experiments which were originally designed for long periods of time are prematurely abandoned because of a lack of funding or changing policies. There are several earlier long-term field experiment trials in Estonia for studying the effect of external causes to forest dynamics, like the application of fertilizers and drainage (Pikk et al., 2001; Valk, 2005), the application of different stand initial densities (Laas, 2001) and the effect of various thinning treatments (Tullus & Reisner, 1998) and the application of different geographical origin (Kurm, 2000). Examples of long-term forest experiments which have been maintained for over a century, providing an uninterrupted series of observations, are the extensive permanent networks maintained by a number of European forest research institutes (Hasenauer, 2006). Such a long-term observational infrastructure is often considered a national asset and is valued nationally but also internationally. The Northern European Database of Long-term Forest Experiments (NOLTFOX) presents a good example for the utilizing the international scientific infrastructure for obtaining the information on long-term field experiments in forestry.

One aspect which has received little attention in the past is the use of previously abandoned field plots: is it worthwhile to “revive” them and to continue with re-measurements after a long time interval of abandonment? Missing data are a part of research, and decisions have to be taken how to deal with them. There are several reasons why particular data may be missing and there are alternative ways of dealing with them (**Paper III**). The re-enumeration of long-term experiments after long periods of neglect represents a particular challenge.

When an experiment is re-established after a long time interval, the challenge is to make use of the entire period of observation, including the observational gap. Accordingly, one objective of this thesis is to define the problem within the general context of forest research, and to

propose a method which can be used to estimate the occurrence of possible disturbance events during the measurement gap.

The question of how to model or estimate the missing data during observational gap has become important. The most common problem in modelling tree growth on irregular measurements is that the time intervals between measurements do not match with desired modelling interval. Often this is solved with the assumption that the periodic increment is constant between measurements and is equal with the average growth rate. In case of concave increment trajectory this assumption leads to underestimation of annual growth (Nord-Larsen, 2006; **Paper IV**). On the other hand using the plot data only with the intervals of undisturbed growth gives us information about the maximum growth rates, but in the long-term predictions for describing the stand development pathways needs the inclusion of the effect of natural and anthropogenic disturbances (**Paper III**).

6.2. Modelling for forest successional descriptions

The disturbance factors that contribute to the dynamics of boreal forest ecosystems are a complex combination of natural factors such as wind, fire, animals, insects, and pathogens together with the anthropogenic influences of forest management, human-induced land use change and pollution (Kuuluvainen, 2002). Disturbances, whether natural or anthropogenic, affect forest structure, composition and ecological processes on a wide range of spatial and temporal scales and on all levels of ecological organization, and are therefore needed to be incorporated into forest development modelling (Stanturf, 2004; Kangur et al., 2004).

Stand density development is one of the most important, but still complicated aspects of forest modelling. The algebraic difference models allow us to predict the average long-term stand development in accordance with a given initial state. The growth models developed in the current thesis predict growth by five-year intervals (**Paper III**) and are therefore inconvenient for the end-user to apply. On the other hand, they are more flexible when taking the limiting line of self-thinning into account. The stands on interval plots used for model parameterizations have not reached the self-thinning state yet and show relatively high basal area and diameter growth. Improving the prediction abilities of these models requires longer intervals of undisturbed development for model calibration.

Stand development predictions in time often depend on reliable height-diameter functions requiring height as the basic input variable (Temesgen & Gadow, 2004). Stand height can be described in several ways: as mean-unweighted, mean-weighted, predominant, top and dominant height. Stand mean height-unweighted (or arithmetic average height) is rarely used, as its estimation requires measuring every tree height in the stand, which is possible to carry out in stands with height not more than 2–3 m (Krigul, 1972). In Europe generalized height-diameter functions have been used since the 1930s. The generalized height diameter function includes both single tree level variables as individual tree heights and diameters, together with stand level variables like basal area and quadratic mean diameter (Gadow & Hui, 1999, Temesgen & Gadow, 2004).

Describing young stand development is a challenge, as growing conditions in young stands are changing rapidly. Still, it is the most crucial period for modelling or for management planning since in this period the stand properties will be set for the entire rotation period. Forest growth modelling in the Nordic and Baltic countries has focused on advanced or mature stands. Very often the growth in early stands is predicted by using the same models as for mature stands. The evaluation of young stand height thus usually leads to over- or underestimation (Huuskonen & Miina, 2007). A classic approach to obtain stand height in advanced stands in Estonia has been to use regression height prediction at the quadratic mean diameter. Accordingly, all tree heights are calculated using the height regression function. Depending on differences in height growth and tree ingrowth in juvenile stands, the time during which a considerable number of seedlings have not reached breast height can be very long (especially in naturally regenerated stands). Therefore, modelling of the height distribution instead of the breast height diameter (dbh) distribution is technically more advisable (**Paper V**). Another important aspect is that the field assessment methodologies also differ for juvenile and advanced stands (Siipilehto, 2009). In younger stands mean height and stem number are assessed. In advanced stands these variables are replaced with basal area, quadratic mean diameter and regression height.

Generally there are currently used in forest growth and dynamics monitoring three different technologies: long-term permanent sample plots, eddy covariance flux towers and dendrochronology (Metsaranta & Lieffers, 2009). In modelling long-term forest dynamics based on long-

term research plots empirical time point descriptions, it is possible to detect or distinguish the changes or irregularities in development (e.g. growth reduction or release of trees, events of tree mortality) (Berg et al., 2006). Still, in most cases these historical time series lack the information about recorded disturbance events and more important about the exact agents causing these events. For the study of causes of individual tree death, the monitoring of single tree death causes has been started in the ENFRP plots in Estonia (Laarmann et al., 2009). These records on the mortality causes will enable in the future to distinguish together with dendrocronological analyse of remaining trees, the effect of particular disturbance agents introduced changes to the post-disturbance development of neighbouring trees (Metsaranta & Lieffers, 2009).

6.3. Management implications

The classical silvicultural operations simplify the stand structure and aim to control or direct the development. The theoretical trends of stand dynamics are presented in Figure 8. The ellipses in Figure 8 are tilted for showing best the centre of location of cutting regimes. The post-disturbance development leads to the mixed, multi-layered stands.

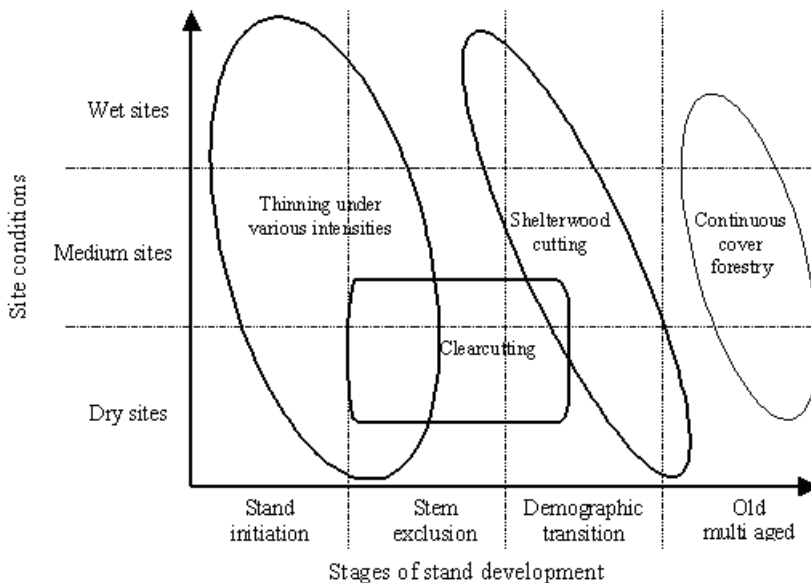


Figure 8. Outlying concept (based on sample plot data) of mimicking natural disturbances with applicable cutting regimes.

Pre-commercial and intermediate thinnings are the main silvicultural operations mimicking natural processes during stand initiation and stem exclusion phases. On dry and fresh sites clearcuttings could simulate heavy natural disturbances in certain cases. On naturally developing stands on wet sites heavy natural disturbances hardly ever occur. Shelterwood cuttings can influence the demographic transition stage and on specific sites clearcutting can be used. On clearcuts some trees and tree groups should be retained to have a more natural disturbance like result. Continuous cover forestry with low intensity selective cuttings is most suitable in mimic natural disturbance patterns during the old multi-aged stage.

Forest management and planning methods (Gadow et al., 2007; Korjus, 2009) integrate assessment of risks and uncertainty into the planning process (Leskinen et al., 2006). The hazard potential includes all the potential threats within a given hazard domain. Potential hazards, their agents and risks can be assessed with probability models as well as in monetary terms (Gadow, 2000). Probability of surviving several hazard factors (survival rate) is multiplicative to surviving each single hazard factor. Such an approach enables to consider many risks in forest management planning.

In both, traditional forest management and management planning for sustaining the yield (Hebert, 2004) but also in management planning for nature conservation (Alexander, 2008) the effect of natural and anthropogenic disturbances is seen and discussed as a threat or possible risk. For evaluating the possible effect of these risk factors several analysis tools have been developed. Some of them already include the effect of natural disturbances or the complex effect of damage (Schelhaas, 2008). Still, if the aim is to manage the forest ecosystems to maintain its ecological characteristics and functions it is necessary to acknowledge the high diversity of naturally existing developmental pathways (**Paper I**). Therefore, for emulating natural disturbances into forest management it is needed to recognize disturbance introduced dynamics as a part of possible management pathways.

6.4. Novelty of study findings for future research

Based on current knowledge and understanding it is widely recognized that long-term series of re-measurements on permanent field plots are ideal data for describing successional changes or for empirical modelling in general. This data has high value for the conceptual modelling, or even more for the testing and evaluating of existing models.

The results of current thesis indicate that in employing the data of long-term permanent field plots for stand development modelling, it is inevitably to take into account the occurrence of natural or anthropogenic disturbances, at different levels of ecological organization. Classically, long-term field plots in forestry have been established to study the effects of varying silvicultural and forest management activities, or to follow the natural development. Often the research plots are considered for exclusion from research plan or for termination after the disturbance occurred on field plots, especially if the disturbing agents can not be identified. Still, for the study of long-term successional dynamics the continuation or re-establishment has high value because of need for long timescale records on ecosystem changes. The data of long-term measurement series always contains some inaccuracies or irregularities that are usually excluded from the further research or analysis. The question of evaluating these irregularities has been inconvenient and there are few studies conducted where these issues are approached (Nord-Larsen, 2006). The method for evaluating the occurrence and extent of the stand affecting disturbances between the two consecutive measurements on the permanent field plots is presented in the thesis. The NG (Eq. 1) describes the disturbance nature. Greater values of NG indicate the occurrence of essential autogenic disturbance event. Low values refer to allogenic processes. This approach allows stands selection with relatively low external effect for long-term modelling.

It is crucial in model simulations to take into account different driving factors in different stand development stages. Important conclusion from my work is that stand development in different stand development stages, described in the conceptual model, must be modelled separately. This conceptual approach was tested and pursued in tree survival estimation study by Sims et al. (2009), where in different stand development stages varying sets of individual tree survival causing factors were proven to be statistically significant. In modelling long-term development it is particularly important that model predictions would be similar and comparable in different stages but also in their overlapping ranges. The stand component

cluster dominant height calculation model for juvenile stands, presents an example for modelling height growth in the young stands with the link to classically used regression height for advanced stands.

Increasingly, modelling aims to describe the effects of processes that operate at an annual timescale. Therefore the information need about the stand development processes and their changes are setting requirements for the observation intervals of long-term observation series. The dendrochronology techniques are important in achieving additional information for modelling annual growth changes and discovering disturbance effects to the forest community long-term development (Metsaranta & Lieffers, 2009). The combined information set of long-term sample plots re-measurements and the detailed time series of the same stand annual diameter and height growth provide good ground for stand development reconstruction, disturbance event analysis and modelling. Long-term observational studies include plots (stands) with quite random initial variation. The initial composition and height distribution predetermines stand development (**Paper II** and **V**). This principle has been also included in elaborated forest models (Hari et al., 2008) and will be pursued in future studies (Kangur et al., 2007).

7. CONCLUSIONS

This thesis addressed different conceptual and methodological aspects of modelling long-term forest dynamics based on the existing permanent field experiments data. As the forest growing conditions and human demands are continuously changing, forest management principles and decision support tools are needed to be adaptive to this continuous change (**Paper II and III**).

For empirical modelling of long-term successional development series of re-measurements on permanent field plots are considered to offer the ideal data. The existing permanent plot data has high value for the conceptual modelling, as well for the testing and evaluating of existing models. The studies presented in the thesis employ three sets of permanent forest experiment data: 1) the early long-term forest experimental series (JLTFE) in Järvselja (growth and yield experiments and thinning experiments), 2) permanent forest growth monitoring plots from the Estonian forest research plots network (ENFRP) and 3) regeneration study plots at Järvselja. Earlier long-term forest growth studies on permanent sample plots in Estonia provide good basis for the long-term successional development studies and the Estonian forest research plots the necessary information for modelling of forest growth and structure (**Paper III, IV and V**). For disturbance studies long-term monitoring sample plots on different disturbance areas should be established to observe disturbance effects on different ecosystem components on different spatial scales (single tree level, stand level and landscape level).

Considering the enormous investment and its usefulness for environmental research, the national importance and scientific relevance of old long-term field research experiments is evident. The method for evaluating the occurrence and extent of the stand affecting disturbances between the two consecutive measurements on the permanent field plots is presented in the thesis (the NG model, Equation 1). For long-term stand development modelling this approach allows evaluating the external effect on permanent plot time series with irregular measurement intervals (**Paper III**).

The data from the permanent growth and yield sample plots was used to develop a conceptual model what can be used to analyze stand development processes on fresh boreal forest type in Estonia (*Oxalis* and

Oxalis-Vaccinium myrtillos site type by Paal (1997)). A theoretical model of forest succession cycles was developed for fresh boreal forest type. Since the dominating stand development affecting factors, mechanisms and their importance vary in different stand successional stages, it is important in stand development modelling to follow and include the factors varying effect into models (**Paper II** and **V**). In comparison with stand development model, Järvelja permanent sample plot data indicates higher production capacity in late-succession stages and lower intensity of management on most studied plots. Cuttings have been mild, mainly deadwood or dying trees were removed. Therefore can be concluded that the cutting regime has reflected (mimicked) the natural development of the stands. A long-term forest successional development scheme with the basic management actions in different stands under different environmental conditions was presented in the work (**Paper II**). The actual trends observed on long-term sample plots were matched with the natural development of stands on similar site types.

In forest modelling one of the most important but still complicated aspects is the prediction of stand density development. The algebraic difference models allow predicting, based on a given initial state, the average long-term stand development. The interval data based growth models predict stand growth by five-year sequence and if the prediction sequence will not fall within the modelling window it is not applicable to the end-user to apply. Nevertheless, for the inclusion of self thinning introduced mortality they are more flexible. An important constraint when using the algebraic difference equations is to avoid long-term predictions in one prediction sequence. Considerable variance in model predictions in comparison of observed values can be expected depending on the differences in initial state of modelling sequence (**Paper IV**).

This study showed that forest management events can mimic natural development of stands quite well (**Paper I** and **II**). Ecological restoration activities could simulate natural disturbances in forests on nature conservation areas. The aim of restoration is always to introduce the necessary initial conditions for predictable natural processes and to transform the heavily human-influenced ecosystem towards natural condition. Nature restoration activities may be used on areas with initial low nature value and where the natural recovery process is expected to be very long. Ecological restoration measures may be also planned on areas where natural disturbances are heavily suppressed or fully excluded by human activities.

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SUMMARY IN ESTONIAN

Metsade pikaajaline dünaamika: püsikatsealade andmestik modelleerimiseks

Doktoritöö käsitleb metsanduslike püsikatsealade andmestikel metsa pikaajalise dünaamika modelleerimise kontseptuaalseid ja metodoloogilisi aspekte. Metsa kasvukeskkonna ja inimühiskonna vajaduste pidev globaalne muutumine tingib vajaduse metsade majandamise kohandamiseks nende muutustega (**artikkel II ja III**). Adaptiivse majandamise kontseptsioon on rakendatav Eesti metsade majandamisel ja korraldamisel.

Doktoritöö tugineb viiele artiklile, milles lähteandmetena on kasutatud 1) Järvseljal asuvate pikaajaliste metsa kasvukäigu ja harvendusraiate katsealade, 2) loodusliku uuenduse püsikatsealade ning 3) Eestit katva metsa kasvukäigu püsiproovitükkide võrgustiku andmeid. Kasutatud on üksikpuu ja puistu kasvu ning struktuuri modelleerimise, samuti puistu pikaageste kasvuridade piiriheduse ja häiringute tuvastamise analüütilist meetodit.

Püsikatsealade mõõtmised kajastavad tegelikke ja reaalseid muutusi metsaökosüsteemis. Aegriidade meetodil on muutused esitatud eeldusel, et vaadeldaval ajahetkel erineva vanusega puistud moodustavad ühe puistu kasvurea. Selline eeldus võib viia moonutatud või ebaõigete järeldusteni, kuna suur hulk dünaamikat mõjutavatest teguritest jääb kirjeldamata. Seetõttu on püsiproovitükkidelt kogutud andmestikud kõrgelt hinnatud mitte ainult kontseptuaalse modelleerimise juures vaid ka olemasolevate mudelite katsetamisel ja headuse hindamisel. Varasemate Eesti pikaajaliste metsanduslike püsikatsealade perioodilistel kordusmõõtmistel kogutud metsa kasvu aegriidade andmed pakuvad piisavalt empiirilist informatsiooni metsa pikaajalise suktsessiooni uurimiseks. Eestit katva metsa kasvukäigu püsiproovitükkide võrgustiku andmed on heaks aluseks puistu struktuuri ja kasvu muutuste modelleerimisel (**artikkel III ja IV**). Erinevatel metsaökosüsteemi osadel ja erinevatel ruumilistel tasemetel (üksikpuu, puistu ja maastik) häiringute mõju uurimiseks ja häiringujärgseks pikaajaliseks seireks on vajalik nii püsiproovitükkide kui ka häiringu sündmuse analüüsi- ja demonratsioonilade rajamine.

Arvestades pikaajaliste katse- ja uurimisalade olulisust loodus- ja keskkonnateaduste uurimisel, on olemasolevad nendest asendamatu teadusliku ja rahvusliku väärtusega ning nende uurimise jätkamine on oluline.

Traditsiooniliselt on rajatud metsanduslikus teadustöös püsikatselasid, uurimaks erinevate metsakasvatustlike ja metsamajanduslike võtete ning looduslike protsesside mõju metsa arengule. Häiringute esinemise järgselt püsikatselad jäetakse, eriti veel juhtudel, kus häiringuagendi ei õnnestu määratleda, kas osaliselt edasisest uurimis- ja mõõtmiskavast välja või loetakse katse antud katselal lõpetatuks. Püsikatseladel mõõtmiste jätkamine või mõõtmiste taastamine omab suurt väärtust metsasuktsessiooni uurimiseks, kus on vajalik pikk ökoloogilisi muutusi ja protsesse kirjeldav andmerida. Püsikatselade andmeridades esineb ebatäpsusi või mõõtmiste ebakorrapärasusi mis hilisema andmetöötluse käigus edasisest andmeanalüüsist välja jäetakse. Selliste ebakorrapärasuste hindamine on tülikas ja ajamahukas tegevus ning seetõttu on antud teemat käsitlevaid uurimusi suhteliselt vähe avaldatud. Doktoritöös pakun välja analüütilise meetodi taastatud katselade ajalooliste mõõtmisandmete alusel ebakorrapärase mõõteperioodide korral seal esinenud võimalike metsamajanduslike tööde ja looduslike häiringute esinemise hindamiseks. Seos NG (valem 1) võimaldab hinnata häiringu iseloomu: allogeensete tegurite mõju peegeldavad indeksi ühest väiksemad väärtused (**artikkel III**).

Erinevas seisundis ja varieeruvate kasvutingimustega puistute pikaajalist arengudünaamikat kirjeldav teoreetiline arenguskeem koos looduslike protsesse matkivate metsamajanduslike tegevuste selgitustega on esitatud **artiklis II**. Puistu arengut mõjutavad peamised tegurid ning nende olulisus varieerub läbi puistu erinevate suktsessioonifaaside, seetõttu on oluline nende muutuste arvestamine ka puistu kasvu modelleerimisel. Pikaajalise metsadünaamika modelleerimisel on oluline jälgida, et erinevat arengufaasi kirjeldavad modelleeritavad tunnused on võrreldavad nii erinevates arengufaasides kui ka nende kattuvatel üleminekualadel. Noorendike keskmise kõrguse arvutamise normatiiv (valem 12, **artikkel V**) on näide noorendike keskmise kõrguse modelleerimisest seotult vanemates puistutes kõrguse arvutamiseks kasutatava klassikalise kõrguskõvera.

Puistu tiheduse muutumine on puistu kasvu modelleerimisel üks olulisemaid, aga ka keerulisemaid ülesandeid. Laialdaselt kasutatavad diferentsmudelid võimaldavad sõltuvalt lähteseisundist modelleerida puistu keskmist kasvu. Eestit katva metsa kasvukäigu proovitükkide mõõtmisandmete põhjal koostatud kasvumudelid võimaldavad prognoosida puistu kasvu viieaastase intervalliga. Juhul kui soovitatav modelleerimise periood erineb viieaastasest tsüklist, on antud andmetel

loodud mudelite kasutamine lõppkasutajale ebamugav. Samas loodusliku väljalangemise või erinevate metsamajandusvõtete simuleerimisel on nende mudelite kasutamine lihtsustatud. Pikaajalist metsa kasvu prognoosimist diferentsmudelitega, kasutades ühte modelleerimise sammu, on soovitatav vältida. Sõltuvalt lähtepunktist, esinevad statistiliselt olulised erinevused mudeli ennustustes võrrelduna tegelike empiiriliste mõõtmiste andmetega (**artikkel IV**).

Järvelja püsiproovialade andmestik võimaldas koostada puistu teoreetilise arengumudeli jänesekapsa ja jänesekapsa-mustika kasvukohatüübi männi enamusega puistutele nii majandatud kui ka majandamata algseisundi korral. Samuti koostasid nende kasvukohatüüpide vanade puistute suktsessioonitsüklite teoreetilise mudeli. Järvelja vanade püsiproovitükkide andmete võrdlemisel Andres Kiviste diferentsmudeli abil saadud puistu kasvuprognoosidega samas kasvukohas, ilmnes Järvelja vanade puistute kõrge puidutootmisvõime hilisemates suktsessioonifaasides madala metsade majandamise intensiivsuse foonil. Uuritud puistutes on raied olnud tagasihoidlikud: valdavalt on raiutud kasvus allajäänuid või surevaid puid. Seega võib väita, et puistu looduslikku arengut järgiva majandusviisi puhul on võimalik säilitada puistute kõrget puidutoodanguvõimet heade kasvukohtade männikutes kõrge vanuseni (**artikkel II**).

Metsade häiringurežiimid ja häiringutega kaasnevad majandamise riskid vajavad jätkuvalt edaspidist uurimist ning saadud tulemused rakendamist metsade majandamisel Eestis. Teadlaste rahvusvaheline koostöö selles valdkonnas võimaldab integreerida sageli lokaalsetest uuringutest saadud teadmisi laialdasemalt: heaks näiteks on Põhja-Euroopa pikaajaliste metsanduslike püsikatsealade andmebaas (NOLTFOX) ja SNSi looduslike metsahäiringute uurimise koostöövõrgustik (SNS Network "Natural Disturbance Dynamics Analysis for Forest Ecosystem Management").

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I

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Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies

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Abstract

• This review summarizes early stand-scale studies of pristine forest structures, disturbance regimes and successional patterns carried out in boreal Eurasia. We attempt to reveal, characterize and classify stand dynamic types that can be used as templates for nature-based forest management.
• The studies reviewed demonstrate multiple successional pathways in stand development in all types of pristine forests. All-aged stands driven by small-scale disturbances are formed over successional development of several hundreds of years. This endogenous development can be interrupted by stand-replacing or partial disturbances leading to successions with even-aged or cohort-structured stands, respectively. In Western Europe, the most common disturbances are windthrows, surface fires and fluctuations in moisture regime; in Eastern Europe and Siberia, the most common disturbances are crown and surface fires and insect outbreaks. Type, return interval and severity of disturbances are strongly influenced by the site conditions and successional stage of a stand.
• Based on characteristics of forest stands and disturbance regime, four main types of pristine boreal forest stand dynamics can be distinguished: (1) even-aged, compositional change dynamics, (2) even-aged, mono-dominant dynamics, (3) cohort dynamics and (4) fine-scale gap dynamics. These types can be mimicked in developing scenarios of ecological sustainable forest management in Eurasian boreal forests.

Résumé – Structure des peuplements, régimes de perturbation et dynamiques de succession dans les forêts boréales eurasiennes : une revue basée sur des travaux russes.

• Cette revue bibliographique résume les résultats de nombreuses études anciennes sur la structure des peuplements forestiers, sur les régimes de perturbation et sur les dynamiques de succession en forêt boréale eurasienne. Une typologie des modes de succession est proposée pour servir de cadre à une gestion forestière proche de la nature.
• Les études analysées montrent l'existence de multiples modes de succession et de développement des peuplements dans tous les types de forêts vierges analysées. Des peuplements mélangés comportant des arbres de tous âges se développent en réponse à des perturbations locales avec des dynamiques de plusieurs siècles. Ce développement endogène peut être interrompu par des renouvellements massifs ou des perturbations partielles qui conduisent à des successions basées sur des peuplements équiennes ou structurés en cohortes, respectivement. En Europe occidentale, les perturbations les plus fréquentes sont les chablis, les incendies de surface et des fluctuations des régimes hydriques ; en Europe orientale et en Sibérie, ce sont les incendies de surface et de canopée, et les attaques massives par des insectes.
• En se basant sur les caractéristiques des peuplements et des types de perturbations, nous avons pu identifier quatre types principaux de dynamiques forestières : (1) une dynamique de changement de composition spécifique avec une structure équienne ; (2) une dynamique de domination par une espèce avec une structure équienne ; (3) une dynamique de cohortes ; et (4) une dynamique de trouées locales. Ces types de succession peuvent servir de base pour le développement de scénarios de gestion forestière durable de ces forêts boréales eurasiennes.

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1. INTRODUCTION

The Eurasian boreal forest belt extends over a huge area from the Russian East to Fennoscandia, covering an area of circa 14 million km². A major part of the global and Eurasian boreal forest is in Russia, covering an area of circa 9 million km². The variation of climate, topography and soils shapes the formation of the various ecological communities (Hytteborn et al., 2005; Nikolov and Helmsaari, 1992). The boreal forest is surrounded by thousands of kilometres of ecotones with bordering ecosystems such as tundra, steppe, peatlands, and meadows. Consequently, there is a wide variety of dynamic processes in a constantly changing environment and interactions between forest and other vegetation types. In the present biogeography of the Eurasian boreal forest, one can also find traces of past climate changes having occurred in the late Pleistocene and Holocene, as well as age-old human impact on the forest cover.

Most parts of the Eurasian boreal forest are affected by intensive forest utilization that has fragmented forest landscapes, changed forest structure and modified disturbance regimes (Granström, 2001; Nordlind and Östlund, 2003; Siitonen, 2001). However, in Russia large intact forested areas driven by natural disturbances still exist in remote locations (Yaroshenko et al., 2001). In most of Eurasia, human impact has increased the annually burnt area, despite modern fire prevention methods. In Fennoscandia, the situation is somewhat different due to efficient forest fire suppression (FAO, 2007).

Historically, the utilization of forests began as selective cuttings both in Scandinavia and Russia. However, with the development of the forest industry harvesting and management based on clear-cutting was entrenched from the beginning (most parts of Scandinavia) or the mid-20th century (Russia, Finland) in all parts of the Eurasian boreal forest. In Russia, shortcomings of the clear-cutting system were revealed from the very beginning, including low profit due to the uneven-aged and uneven-sized structure and low quality of wood in the pristine forests, and the detrimental ecological consequences of massive clear-cuts (Kravchinsky, 1901). As a result, in the 1950s selective cuttings were recommended and new systems of selective cuttings were developed and applied in practice (Tkachenko, 1931; Voropanov, 1950). These cuttings, especially in uneven-aged low-productivity northern forests, were designed by analogy with modern thinnings, aiming at increasing the productivity, resilience and health of forests. The most weakened trees as well as the largest dominant trees that could not increase their increment after improvement in growth conditions were cut. However, in practice the implementation of these selection systems was limited.

In the early 20th century, there was an increased demand for knowledge of the distribution of timber resources as well as the structure of forests to fulfill growing timber consumption (Ivessalo, 1937). In Scandinavia at that time, the first research steps were taken to describe, classify and understand the structure and development of forests (e.g. Aaltonen, 1919; Arnborg, 1943; Ivessalo, 1937; Sernander, 1936; Sirén, 1955). In Russia, the theoretical concepts of forest- and soil-forming processes, as well as landscape dynamics, were developed (see

review by Utkin, 1999). The first studies on the growth, structure and regeneration of northern forests and attempts at their classifications were conducted by Mal'gin (1842), Vargas de Bedemar (1850), Timofeev (1894), Pole (1906), Bitrikh (1908) and Sokolovsky (1908). Pole (1915) listed 4291 references on forestry, botanical and geographical topics published in northern Russia and Finland. The growth and yield tables for oak (*Quercus*), pine (*Pinus*), spruce (*Picea*) and birch (*Betula*) forests compiled by Vargas de Bedemar (1850) have not yet lost their importance.

The first empirical findings were mainly static and qualitative descriptions of tree species composition, age structure and diameter distributions (e.g. Kozachenko, 1912; Ivashkevich, 1915). Later the focus was shifted to stand development, and conceptual and quantitative schemes of stand dynamics were constructed, based mostly on the chronosequence approach (Alekseev, 1948; Bogoslovsky, 1921; Ivessalo, 1937; Sirén, 1955; Voropanov, 1950). More recently, these previous findings and associated systems of classifying stand dynamics were synthesized (Dyrenkov, 1984; Melekhov, 1980).

Currently, the attempts to develop sustainable forest management call for better understanding of natural forest structure and dynamics. Knowledge is needed on central ecological characteristics and processes in the natural forest, such as structure, composition, disturbances, regeneration and successional dynamics (Attiwill, 1994; Kuuluvainen, 2002). For example, the question as to what extent forests are naturally even-aged or uneven-aged has been debated since the 19th century. This issue is related to the type of prevailing disturbance regime, i.e. whether highly severe stand-replacing disturbances or less severe partial disturbances naturally dominate. These issues are important also from the practical point of view. For example, arguments for the natural predominance of stand-replacing disturbances and even-aged stands have been used to legitimize clear-felling as a natural management system (Sirén, 1955; Valyaev, 1984). On the other hand, where less severe disturbances are the norm and pristine stands are mostly uneven-aged, selective cutting should be promoted if the aim is to maintain the structure and ecological characteristics typical of the forest site type (Dyrenkov and Shergol'd, 1973; Kuuluvainen, 2002; Volkov, 2003).

Differences and similarities in structure and dynamics of Western and Eastern European forest vs. Siberian forest have not been discussed so far. In Russian terminology the taiga forests are classified into two broad types. The so-called dark coniferous taiga consists of *Picea abies*-dominated forests in Western Europe and poly-dominant *Picea abies*, *P. obovata*, *Abies sibirica* and *Pinus sibirica* forests in Eastern Europe and Siberia. The so-called light coniferous taiga is composed of *Pinus sylvestris* and *Larix* spp.-dominated forests. The number of dominant tree species increases in dark coniferous taiga from West to East.

This review is an attempt to summarize original stand-scale studies of pristine forest disturbance regimes and successional patterns carried out in boreal Eurasia. A large part of the reviewed studies are written in Russian, and most of them have not been included in earlier reviews (Angelstam, 1998; Angelstam and Kuuluvainen, 2004; Gromtsev, 2002;

Kuuluvainen, 1994, 2002). The review is also used to synthesize and classify different types of structure and dynamics characteristic of pristine boreal forest stands. We hypothesized that differences in disturbance regimes and site conditions lead to different types of stand structures and dynamics in Eastern Europe and Siberia compared with Western Europe, and in dark-coniferous taiga compared with light-coniferous taiga. Finally, we discuss the implications of this knowledge for ecologically sustainable management. Although the research methods in some of these older Russian and Scandinavian studies on forest structure and development may not meet modern standards, it is believed that the early observations may inspire new research and give answers to topical questions related to the ecology and sustainable management of the boreal forest.

2. GENERAL CHARACTERISTICS OF EURASIAN BOREAL FOREST ECOSYSTEMS

2.1. Climate, soils and tree species

The climate in boreal Eurasia is characterized by long cold winters and short, rather warm and sunny summers. The mean annual temperature and precipitation are low. However, there is considerable variation, depending on the latitude, maritime-continentality gradients, and local topography. In continental areas such as central Siberia, winter temperatures fall to $-50\text{ }^{\circ}\text{C}$; the mean temperature in July varies between $10\text{ }^{\circ}\text{C}$ and $22\text{ }^{\circ}\text{C}$; the annual precipitation amounts to between 300 and 600 mm. In the European boreal forest, Atlantic influence and cyclones result in a milder climate with more rain and instability than in the continental regions of Eurasia (Hytteborn et al., 2005).

Soil formation is characterized by the podzolization process: the acidic reaction of decomposing litter causes leaching and moving of minerals in topsoils, resulting in a light horizon below the forest floor (Kaurichev et al., 1989). A fine-grained pattern of lowland forests and wetlands is formed (Hytteborn et al., 2005) where a positive precipitation–evapotranspiration balance, together with low decomposition rates due to low soil temperatures, leads to humus and peat accumulation. In the northernmost areas with the lowest mean annual and winter temperatures, permafrost prevails. Forests can grow where the permafrost melts to a depth of 1 m during the growing season. The presence of permafrost also leads to the development of palsas and peat plateaus (Bhiry et al., 2007).

The dominant tree species belong to *Abies* (mainly *A. sibirica* Ledeb.: Siberian fir), *Larix* (mainly *L. gmelinii* (Rupr.) Rupr.: Dahurian larch, *L. sibirica* Ledeb.: Siberian larch, *Picea* (mainly *P. abies* (L.) H. Karst.: Norway spruce, *P. obovata* Ledeb.: Siberian spruce) and *Pinus* (mainly *P. sylvestris* L.: Scots pine, *P. sibirica* Du Tour or (Loudon) Mayr.: Siberian pine) genera. Deciduous species (*Betula pendula* Roth.: silver birch, *B. pubescens* Ehrh.: downy birch, *Populus tremula* L.: aspen, *Alnus incana* (L.) Moench.: grey alder, *A. glutinosa* (L.) Gaertn.: black alder) are represented, particularly after disturbances such as fires or windstorms.

Life history characteristics determine the successional sequence of the tree species at a particular site. The Russian word ‘taiga’ was first associated with the coniferous forests of Siberia. Today, the word has acquired a more general meaning denoting the coniferous forests of the Northern Hemisphere. Different classifications of vegetation zones describe regional variation, dividing the Boreal Zone latitudinally into subzones and longitudinally into sections. Three vegetation zones (northern, middle and southern) are widely recognized (Ahti et al., 1968). Northernmost forests are composed by Dahurian larch, Siberian spruce and Scots pine. Also hardwoods are represented here: e.g. *Betula pubescens* ssp. *tortuosa*. In south of boreal forests, the importance of hardwoods increases, and nemoral species may appear in co-dominance. Boreal forest transition areas are dominated by coniferous species with admixtures of temperate (nemoral) hardwoods, including pedunculate oak *Quercus robur* L., ash *Fraxinus excelsior* L., European white-elm *Ulmus laevis* Pall., Wych elm *U. glabra* Huds., beech (*Fagus sylvatica* L.), Norway maple *Acer platanoides* L., lime *Tilia cordata* Mill. This zone is the boreonemoral or hemiboreal (Ahti et al., 1968). Ecotones among the northern coniferous forests are detected with mountains or grasslands. In the north the boreal forest undergoes a transition with the tundra vegetation type. The ecotone of the forest-tundra is a belt between the taiga and treeless tundra.

2.2. Disturbance factors

Fire has long been acknowledged as a crucial factor shaping boreal forest structure and development (Melekhov, 1947; 1948; Niklasson and Granström, 2000; Saari, 1923; Sirén, 1955). There is wide variability in fire behaviour and regimes, from infrequent high-severity stand-replacing fires to frequent low-severity surface fires. The human impact on fire regimes also differ. Depending on the region, 3–70% of fires in boreal Eurasia are natural fires, i.e. ignited by lightning (Ivanov, 1996; Gromtsev, 2002).

The ‘natural’ fire regimes vary in different parts of the Eurasian boreal forest (Buryak et al., 2003; Furyaev, 1996; Gromtsev, 1996; 2002; Sofronov and Volokitina, 1990; Valendik and Ivanova, 2001). It has been estimated that the mean frequency of fires in Russia’s European boreal forests vary from 1–2 per century to 1–2 per millennium (Gromtsev, 2002).

The forest fires, burnt areas, and fire hazards of forest stands and landscapes have been classified by Melekhov (1947) and Furyaev (1996). The type of fire, i.e. crown, surface or ground (in peatlands), and its severity are determined by a complex set of factors, including weather conditions (mostly humidity and wind speed), type of forest community (structure, composition and stock of flammable materials), time since and type of previous fire (Furyaev, 1996; Kurbatskij, 1964; Melekhov, 1947). According to Melekhov (1947), surface fires comprises 76–86%, crown fires 16–24% and ground fires 0.1% of the total number of fires in the European Russian boreal forest. In Siberia, 87% of fires are surface, 12% are crown and 1% is peatland ground fires (Buryak et al., 2003).

In Siberian forests, two principal fire regimes were described by Valendik and Ivanova (2001). Low frequencies of fires are characteristic of moist 'dark coniferous' forests dominated by Siberian spruce, Siberian fir and Siberian pine in Western Siberia. In contrast, the high flammability and high frequency of fires are typical for low-mountain 'light coniferous' forests dominated by Scots pine and Siberian larch in Eastern Siberia. Of the total number of fires in Siberia, most (83%) occur in Eastern Siberia and the Far East, whereas only 17% occur in Western Siberia (Valendik and Ivanova, 2001). Gorshkov et al. (2004) detected a dichotomy in the fire disturbance pattern in the Kola Peninsula and Karelia: the fires were either low-severity (less than 33% of the basal area of the trees killed) or high-severity (over 67% of the basal area of trees killed).

The concept of 'fire maturity' (Kurbatskij, 1954) deals with the probability that fire emergence gradually increases after snowmelt in the spring or after rainy periods in the summer, associated with the drying of fuels. The fire hazard can be predicted based on the fire maturity characteristics of a forest ecosystem (Furyaev, 1996). Fire maturity refers to a certain moisture level determined by type and stock of fuel and attained after drying for a certain number of days after rain. Fire maturity in the Boreal Zone of European Russia, the Western Siberian Plain and Middle Siberian Plateau, is dependent on forest type, tree species composition and successional stage of a stand, as well as on the landscape type (Kurbatskij, 1964). Burnt forests have been classified according to ecosystem legacies, such as living trees, snags and fallen trees in the northern forests of European Russia (Melekhov, 1948), Siberian pine – broadleaved forests of the Far East (Soloviev and Solodukhin, 1953) and Scots pine and Siberian larch forests in southern Yakutija (Scherbakov and Chugunova, 1960).

In addition to fire, various non-pyrogenic disturbance agents have been recognized as important factors in pristine boreal forests. Wind was demonstrated as a crucial factor shaping the structure and dynamics of the boreal forest (Sernander, 1936; Skvortsova et al., 1983; Turkov, 1985; Ulanova, 2000). The sizes of gaps formed after low- or moderate-severity windthrows can vary from 100 to 10 000 m² (Skvortsova et al., 1983). A dichotomy of the pattern of tree mortality and consequent regeneration recruitment was revealed: either an even or wave-like pattern, depending on disturbance severity (Skvortsova et al., 1983; Pugachevsky, 1992). Polyakov and Semechkin (2004) described cohort-replacing windthrows in Siberian pine stands. Partial mortality of dominant cohorts in the southern boreal spruce forests induced by fluctuation of moisture in the topsoil layer was described by Vygodskaya et al. (2004).

In general, insects, fungal and bacterial diseases have not caused large-scale disturbances in pristine and seminatural European boreal forests (Storozhenko et al., 1992; Storozhenko, 2004), but as 'internal' or chronic disturbance agents they cause formation of gaps (Morozov, 1925; Voropanov, 1950). In contrast, biotic disturbances play an important role in Siberia, often 'substituting' for windthrow as a disturbance agent in late-successional stands. For example, in the Irkutsk

region during the period 1870–1963 circa 1, 061 million ha of Siberian pine forests died due to attack by the Siberian silk moth *Dendrolimus sibiricus superans*. During the last 40 years outbreaks of this pest were registered in the area of 1 465 000 ha (Vaschuk and Shvidenko, 2006). The main host of this insect is Siberian pine and, to a lesser extent, larch, fir, spruce and pine. The impact of these outbreaks is most severe when followed by fires (Furyaev, 1970), because of high fuel loads of standing dead wood (Verkhunov, 1970).

Other insects able to cause significant forest dieback include dingy larch bell (*Zeiraphera dimiana*), saddleback looper (*Ectropis crepuscularia*), as well as secondary pests: six-toothed bark beetle (*Ips sexdentatus*), eight-toothed bark beetle (*I. acuminatus*), pine shoot beetle (*Tomicus piniperda*), lesser pine shoot beetle (*Tomicus minor*), longhorn beetle (*Spondylis buprestoides*), great spruce bark beetle (*Dendroctonus micans*) and Pissodes weevil (*Pissodes piniphilus*) (Prozorov, 1929).

Gap-phase disturbances caused by death of individual trees or small groups of trees drive the mosaic structure and regeneration dynamics of old-growth forests in the absence of catastrophic disturbances (Hofgaard, 1993; Hytteborn and Packham, 1985; Kuuluvainen et al., 1998; Leemans, 1991; Liu and Hytteborn, 1991; Skvortsova et al., 1983).

3. CONCEPTUAL, THEORETICAL, AND METHODOLOGICAL ISSUES

In older literature, many of the views and concepts have a different meaning compared with modern usage. Some phenomena were discussed but were not placed in a theoretical context. For example, the concept of *disturbance* was not used in the older literature, although the dynamic nature of forests was acknowledged from the very beginning (e.g. Ivashkevich, 1915). Therefore, when referring to the older concepts and terms, we have given their modern interpretation.

Attempts to develop universal scientific theories were typical for the early 20th century. For example, in Finland, the forest site type theory developed by Cajander (1909; 1926) has been influential in forest science around the world. This classification system is based on the assumption that competition leads to well-predictable plant community structures determined by the plants' properties and the 'primary' site conditions (Oksanen, 1990). In Russia, the concept of the 'forest-forming process' has been and still is an important and over-arching framework for studies in forest structure and dynamics (Anonymous, 1991; Morozov, 1912, 1925; Utkin, 1999). Studies carried out in the framework describe the interrelationships between forest-forming factors and ecosystem processes and types of stand structures and dynamics.

3.1. The conceptual framework of the 'forest-forming process' in Russia

The concept of the "forest-forming process" was introduced by Morozov (1912; 1925) and theoretically grounded

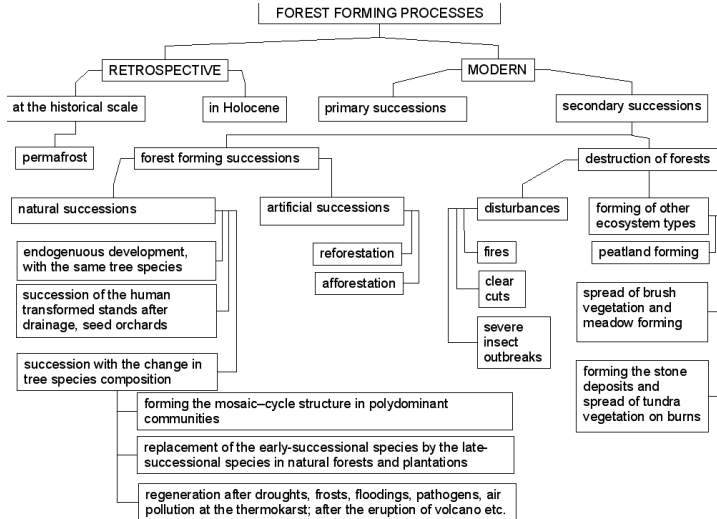


Figure 1. An illustration of the elementary processes that are united by the framework of ‘forest-forming process’. Constructed from Utkin (1999) using different approaches for analyzing the forest-forming process: retrospective (biogeography of forests in the Holocene), historical (human impact from ancient times) and modern (current changes in dynamics of forest ecosystems).

by Kolesnikov (1956). Morozov examined the main factors that ‘form’ forests, i.e. factors that affect forest characteristics and development. He developed a doctrine for species replacement and outlined ways of using the peculiarities of the forest-forming process in the classification of forest vegetation. Morozov (1912; 1925) concluded that the main forest-forming factors are: (1) biological characteristics of tree species, (2) factors of the geographic environment (climate, bedrock, relief and soil), (3) the forest plant community itself, or ‘biosocial’ relationships, (4) the animal community; (5) historical-geological factors and (6) the human impact. He recognized the characteristic features of the process:

- viz. intensity and character of interrelations between tree species in forest communities (competition, mutualism etc.);
- degree of modification of a site by an ecological community (ecological engineering; or reaction according to Clements 1916);
- the degree of ‘fitness’ of organisms relative to each other and to environmental conditions;
- direction and intensity of natural selection in a community.

Morozov (1912) also suggested an analogy between the forest community and an organism, calling the former a ‘social organism’. This idea was analogous to the view of plant communities as ‘superorganisms’ by Clements (1904; 1916). However, in contrast to Clements who believed communities converge through succession from initially distinct, environ-

mentally determined starting points towards a climax vegetation, the characteristics of which are solely controlled by the regional climate (the climatic climax), Morozov (1912; 1925) acknowledged the influence of various factors, i.e. the forest-forming factors, multiple pathways of succession and continuous change in forest communities.

Kolesnikov (1956) treated the forest-forming process as the totality of all phenomena affecting the characteristics and dynamics of forest communities, including colonization, establishment, growth, die-off and changes in “phytocoenoses” (plant communities). Vegetation and soil development were considered as interacting processes and their changes as thus coinciding. Later Utkin (1991), based on the works of Kolesnikov (1956) and Smolonogov (1968; 1990), suggested different approaches for analyzing the forest-forming process: retrospective (biogeography of forests in the Holocene), historical (human impact from ancient times) and modern (current changes in dynamics of forest ecosystems) (Fig. 1).

Kolesnikov (1956) and Smolonogov (1999) considered forest forming as a cyclic process that consists of a sequence of quantitatively different periods, stages and phases. They believed that each forest community represents a link in the chain of vegetation development at a site. Exogenous factors can influence stage rotation. Severe stand-replacing disturbances, particularly fire and clear-cutting (Sedykh, 1991) and windthrow (Smolonogov, 2000), lead to appearance of secondary communities, including non-forest communities with specific dynamics. Man’ko (1996; 2004), working in

the Russian Far East, concluded that the stages in a forest-forming process are dependent on the characteristics of forest ecosystems, type of exogenous abiotic factors and the impact (severity) of disturbance.

3.2. Methodological considerations

Attempts to answer basic questions, and create qualitative descriptions and general theories of phenomena, were typical of the early studies. The outcomes (schemes, general trends, conclusions) were often based more on intuition and extensive field experience, than on empirical data obtained via rigorous sampling procedures as used in modern research. Instead the approach was mainly descriptive. Sampling, if carried out, was mostly subjective and poorly documented.

Many later studies (e.g. in the 1980–1990s) were designed, based on the previously established dominant theoretical frameworks such as the theory of the forest-forming process in Russia and Cajander's theory of forest site types in Finland. These studies provided quantitative descriptions of the structure and dynamics of the boreal forest, based on more rigorous methodologies. For example, in the early Russian studies of uneven-aged stands the size of sample plots was determined in order to measure a minimum of 200 trees of the main 'element of forest', a cohort of trees regenerated within a 40-year period. In practice, this means a sample plot of at least 0.5 ha; all trees on the plots were numbered and measured, and statistical parameters were calculated (Dyrenkov, 1984; Kazimirov, 1971; Zybchenko, 1984).

Most early works on stand development were based on the chronosequence approach, whereas in later research the combination of chronosequence with observations on permanent sample plots, representing only partial substitution of time by space, was applied (Dyrenkov, 1984; Fedorchuk et al., 1998). Despite the shortcomings in research methodology from the modern point of view, the historical studies on structure and dynamics provide an important source of information for generalizing pattern and processes in the boreal forest. This information may also be used to generate hypotheses that can be tested through modern scientific methods. Indeed, this was done to some extent in later publications.

4. STAND STRUCTURE AND DYNAMICS

4.1. Age structure of pristine forest stands

In Russia, contrasting views of the natural age structure of boreal forest stands have been presented. In the late 19th and early 20th centuries, a general view prevailed that northern forests are naturally even-aged, i.e. stands consist of only one 'element of forest': a single tree age cohort (cf. reviews by Dyrenkov, 1984; Pugachevsky, 1992; Volkov, 2003). However, the opposing view that a pristine forest is naturally uneven-aged was also presented at the same time. Bogushevsky (1912) argued that the closer the forest is to its primeval state, the

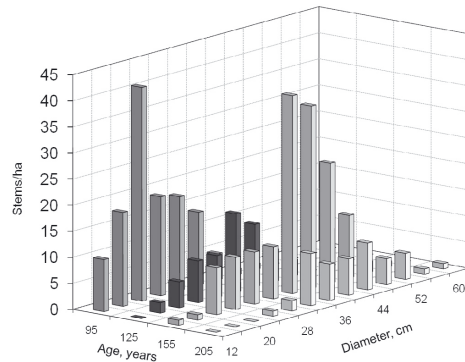


Figure 2. An example of the distribution of trees (ha^{-1}) by diameter and age classes in an uneven-aged Norway spruce (*Picea abies*) forest in the Novgorod region, the southern Boreal Zone (constructed from Kozachenko (1912), sample plot # 4, on drained loam, average tree height 28 m; trees larger than 8 cm in DBH were measured).

more it is a mixture of trees of different age and size; a pristine forest lives, dies and regenerates in small patches.

The first quantitative empirical data documenting the uneven-agedness of pristine forests were presented on the descent of foresters of the Arckangelsk region in 1912. Kozachenko (see Orlov, 1927) presented two-dimensional distributions of tree age and diameter for a Norway spruce forest (Fig. 2). The figure illustrates the general pattern in which the young and small trees are most abundant and the number of trees declines with tree age and size. However, each size class contained trees of various ages.

Ivashkevich (1915) illustrated the structure of a pristine forest with an example of the Siberian pine forest. Uneven-agedness together with spatial patchiness were recognized as the main features. This pattern was a consequence of the periodicity of regeneration and the very slow growth of the trees during the first app. 100 years and then growth release due to gap formation. Ivashkevich (1915) discussed the role of natural disturbances (wind, fire or insects) in decreasing the predominance of coniferous trees and converting stands into mixed species stands. This was probably one of the earliest documentations acknowledging the importance of natural disturbances in forest ecosystems (Ivashkevich, 1915).

These early studies and debates about the 'natural' age structure of European boreal forests were synthesized by Orlov (1927), who stated that between the two extremes, even-aged and all-aged forest stands, there is a continuous number of transitions. Orlov indicated that even-aged forests originated either after stand-replacing fires or windthrows. Ivashkevich (1929) drew the same conclusions for forests in the Far East.

In Finland, the studies based on the national Finnish forest inventory data from the early to the mid-20th century point

out the general uneven-sized character of natural and seminatural stands (Lähde et al., 1991). In Russia, the general dominance of complex structures and uneven-agedness of natural spruce forests was confirmed by Svalov (1961), Valyaev (1961) and Jakovlev (1983). The uneven-aged structure of fir-dominated forests was demonstrated by Shavnin (1959) and Smolonogov (1960). The structure of uneven-aged Scots pine (Aaltonen, 1919; Buzykin, 1967; Huse, 1964; Shanin, 1967; Verkhunov, 1979), Siberian pine (Povarnitsin, 1944), Siberian larch (Povarnitsin, 1941, 1944; Shanin, 1967) and Korean pine *Pinus koraensis* (Siebold & Zucc.) (Moiseenko, 1967) forest stands in Siberia was described in detail. At the same time, Dekatov (1961), Pobedinsky (1961) and Melekhov (1962) recognized the existence of both even-aged and uneven-aged pine forests in the European North. The revealed high variability of pristine boreal forest age structure suggested a need of classification reflecting successional status of stands.

4.1.1. Classifications of stand structures

Classifications of pristine forest stand structures are useful in assessing, for example, landscape patterns and proportions of stand successional stages. In Russia, early attempts to classify forest stands by age structure were performed by Sinelschikov (1958) and Gusev (1964). A conference on uneven-aged forests in the Urals, Siberia and Far East, held in Krasnoyarsk in 1967, summed up the attempts at classification of forest stand structures (Anonymous, 1967). The main conclusion of contributing participants of discussion was that the classification should take into account the stand dynamics and conditions that affect formation of the forest structure. This approach was later consolidated by Dyrenkov (1984). The main types of tree age structures based on tree distributions in 40-year-wide age cohorts (corresponding to a single "element of forest") were distinguished by Dyrenkov (1984) as follows (Fig. 3):

1. Relatively even-aged stands (from here on referred to as **even-aged**). The age variation of the overstorey trees does not exceed 40 y. The diameter and age distributions are unimodal, and near-normal.
2. Absolutely uneven-aged stands (from here on referred to as **all-aged**). All 40-year groups of the predominant tree species population up to the lifespan are present, but none exceeds 40% of the total biomass. The diameter and age distributions are "negative-exponential" or "reverse J-shaped". The following subtypes are distinguished:
 - 2.1 Tree age spatial distribution is even.
 - 2.2 Tree age spatial distribution is patchy.
3. Relatively uneven-aged stands (from here on referred to as **uneven-aged**). The population of the predominant tree species is continuous up to over 200 y, but 50–90% of the total biomass is concentrated in one of the 40-year-old cohorts. The tree diameter and age distributions are multimodal, i.e. with several peaks. The following subtypes are distinguished:
 - 3.1 Young cohorts predominate; stands regenerate after disturbance.

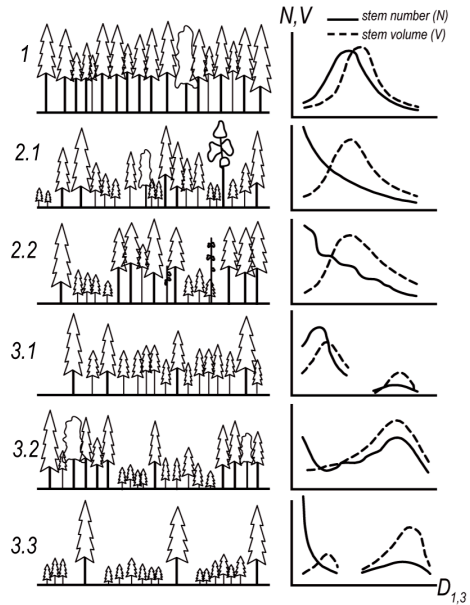


Figure 3. Tree age and diameter distributions in stands with different age structure types (redrawn from Dyrenkov, 1984). 1: Even-aged stands, 2.1: All-aged stands with even distribution of trees, 2.2: All-aged stands with patchy distribution of trees, 3.1: Uneven-aged stands with a dominance of young cohorts, stands regenerated after disturbance, 3.2: Uneven-aged stands with a dominance of old cohorts, process of gradual die-off of the main cohorts, 3.3: Uneven-aged stands with a break in regeneration dynamics.

- 3.2 Old cohorts predominate; the main cohorts gradually die off.
- 3.3 Tree age distribution is not continuous; break in regeneration chain.

4.1.2. Influence of site conditions

The importance of site conditions and forest stand conditions, such as tree age and diameter distributions, spatial structure and successional pathways, affecting the characteristics of stand structure and dynamics, have been verified in several studies (Dyrenkov, 1984; Korchagin, 1956; Tolmachev, 1954). Dyrenkov (1984) (Fig. 4) showed that all-aged spruce stands could be formed only in the following forest site types: *Piceetum myrtillosum* (medium moist and fertile sites), *P. polytrichosum* (low fertility, high moisture sites, paludification by groundwater), *P. myrtilloso-polytrichosum* (transition between the two previous types), *P. sphagnosum* (very

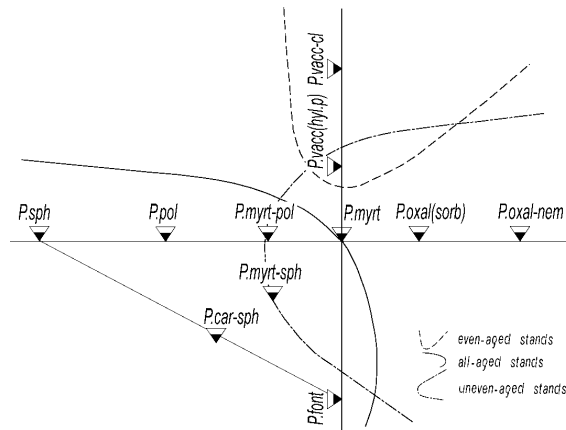


Figure 4. Interrelationship between the main types of tree age structures of pristine spruce stands and forest site types of a plain taiga shown on the 'Sukachev's cross' – a system to classify boreal forest types. The changes on environmental variables on the axes are presented as follows: the crossing of axes refers to average growth conditions on sites; right from crossing is increase in soil moisture, better drainage and soil fertility (from *Myrtillus* to *Oxalis nemoralis* forest type); left from crossing is increase in soil moisture, but poor drainage and low fertility, paludification (from *Myrtillus* to *Sphagnum* forest type); upwards from crossing is decrease in soil moisture and in soil fertility (from *Myrtillus* to *Vaccinium* forest type); downwards is increase in soil moisture and paludification by groundwater (from the *Myrtillus* to fern forest types). The triangles determine the positions of the site types according to the classification. *P. vacc.-cl.*: *Piceetum vaccinioso-cladinosum*, *P. vacc. (hyl. p.)*: *P. vacciniosum* (var. *hylocomiosum purum*), *P. myrt.*: *P. myrtilloso-hylocomiosum*, *P. oxal. (sorb.)*: *P. oxalidoso-hylocomiosum* (var. *sorbosum*), *P. oxal.-nem.*: *P. oxalidoso-nemoritherbosum*, *P. myrt.-pol.*: *P. myrtilloso-polytrichosum*, *P. pol.*: *P. polytrichosum*, *P. sph.*: *P. sphagnosum*, *P. myrt.-sph.*: *P. myrtilloso-sphagnosum*, *P. car.-sph.*: *P. caricoso-sphagnosum*, *P. font.*: *P. fontinale*. Redrawn from Dyrenkov (1984).

nutrient poor, very moist sites, paludification by precipitation), *P. myrtilloso-sphagnosum* (transition type), *P. caricoso-sphagnosum* (nutrient-poor sites, paludification by both precipitation and groundwater) and *P. fontinale* (fertile, moist sites, usually situated near bodies of water). Three forest types, the *Myrtillus* group viz. *Piceetum myrtillosum*, *P. myrtilloso-polytrichosum* and *P. myrtilloso-sphagnosum*, could also form uneven-aged stands. Uneven-aged stands could also be associated with the following forest types: *Piceetum oxalidoso-hylocomiosum* (medium to high fertility sites, good moisture regime) and *P. oxalidoso-nemoritherbosum* (the highest fertility in spruce forests, good moisture regime). *P. vacciniosum* (nutrient-poor sites, dry) and *P. vaccinioso-cladinosum* (the poorest, very dry sites) could form only even-aged stands due to concurrent surface fires and consequent replacement of spruce by pine (Dyrenkov, 1984).

Abaturov et al. (1988) and Falaleev (1985) documented a variety of types of stand age structure in European and Siberian southern boreal forests. Verkhunov (1970) showed that in Western Siberia and the Baikal region the spatial structure of uneven-aged Scots pine stands depends on site conditions. The stands growing on dry sands and fine sandy loams (e.g. *Pinetum lichenosum*) have patchy tree age distribution, whereas on fresh sandy and loamy soils (e.g. *Pinetum myrtillosum* and *P. herbosum*) the distribution is more even. Ermolenko (1967) associated the age structure of Scots

pine forests in the Sayan Mountains with altitude and forest type: the foothill forests (especially of the *Pinetum vacciniosum* type) are more uneven-aged than the mountain forests.

The variation in tree diameter and age distributions of Norway spruce stands under various site conditions is shown in Figures 5 and 6 (Dyrenkov, 1984). Distinct age cohorts are most pronounced in spruce stands growing either on fertile (*Tiliosum*, *Magnofilicosum*) or poor and dry (*Vacciniosum*) sites. The ages of the oldest spruce cohorts do not exceed 240 years (Dyrenkov, 1984). The stands susceptible to periodic windthrows are those of tall spruce trees with large crowns but shallow root systems. In dry stands, spruce is usually eliminated by low-intensity fires that favor regeneration of pine. *Piceetum myrtilloso-polytrichosum*, *P. myrtilloso-sphagnosum* and *P. myrtillosum* sites are characterized by fine-scale gap dynamics and have tree age structure closer to all-aged. Spruce cohorts older than 360 years are present (Fedorchuk et al., 1998; Volkov, 2003).

The studies reviewed demonstrate that the age structure and regeneration dynamics of forests are influenced, among other factors, by site conditions. Pristine forests develop towards an uneven-aged structure, but stand-replacing disturbances can reset them into an even-aged state. Age structure is the first key for understanding stand successional pathways under different disturbance regimes. Even-aged stands are indirect evidence of stand-replacing disturbances. Uneven-aged stands develop

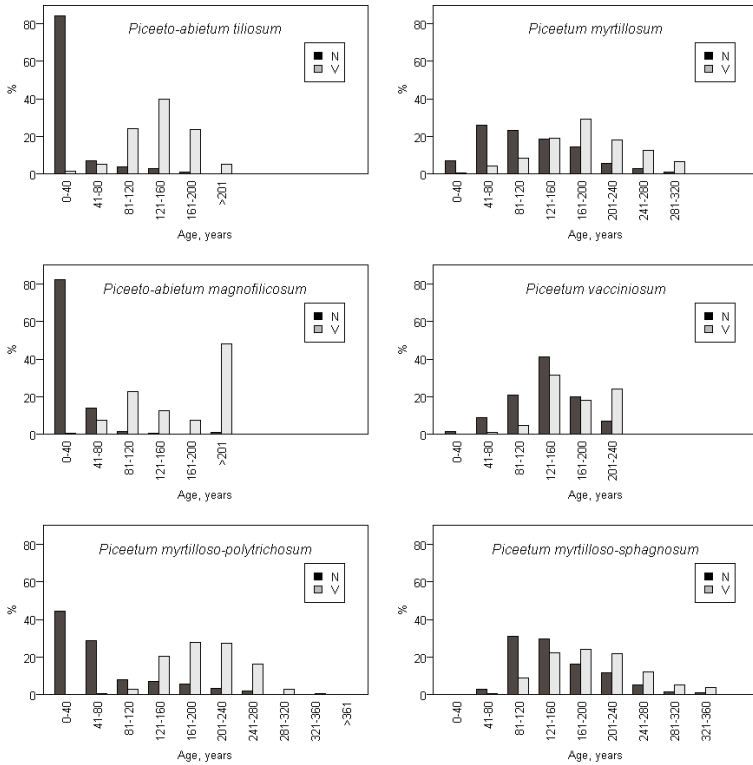


Figure 5. Age structures of pristine boreal spruce stands in different forest types. V: volume, $m^3\ ha^{-1}$; N: number of trees per ha. The figures for *Piceeto-abietum tiliosum* (Middle Prikamye), *Piceeto-abietum magnificosum* (Visherskoye Preduralye), *Piceetum myrtilloso-polytrichosum* (midriver Vychedga) were constructed from the data of Dyrenkov (1984); those for *Piceetum myrtillosum* (Karelia) and *Piceetum vacciniosum* (Karelia) were constructed from the data of Volkov (2003), that for *Piceetum myrtilloso-sphagnosum* (northeast of the Leningrad region) was constructed from Fedorchuk et al. (1998). See the ‘Sukachev’s cross’ in Figure 4 for ecological characteristics of the forest types.

after partial cohort-replacing disturbances, with the ratio between younger versus older tree cohorts indicating disturbance severity. All-aged stands develop over several centuries of succession in the absence of significant disturbances.

4.2. Successional pathways of stand development

4.2.1. Dark coniferous taiga

Dark coniferous taiga forests are formed by Norway spruce-dominated forests in Western Europe and poly-dominant Norway spruce, Siberian spruce, fir, Siberian pine forests in Eastern Europe and Siberia. In Russia, the first empirical data describing the development of dark coniferous taiga forests

were presented in the growth tables compiled by Vargas de Bedemar (1850). Bogoslovsky (1921) demonstrated the structure of an uneven-aged Norway spruce forest as a basis for studies on increment and regeneration. The development of spruce forests originating after fires or clear-cuts was quantitatively characterized in the 1960s for many northern regions in growth tables of pure even-aged spruce and pine as well as of mixed spruce-deciduous and deciduous-spruce forests (the former group dominating) (Gorsky, 1962; Ilvessalo, 1967; Kurzin, 1958; Levin and Gusev, 1958; Maksimov, 1967; Ogorodov, 1951).

The motivation for the early studies was often to reveal regularities in forest dynamics that could be used in developing silvicultural practices for timber production (Sirén, 1955; Ilvessalo, 1920; 1970). For this, the central tendency in stand

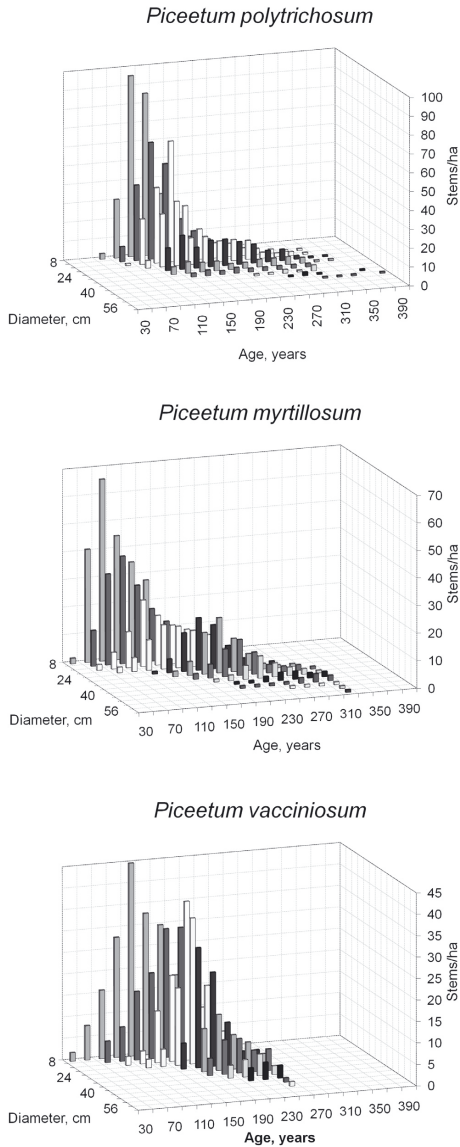


Figure 6. Averaged tree age and diameter distributions for *Piceetum polytrichosum*, *P. myrtillosum* and *P. vacciniosum* sites, Karelia (constructed from the data of Volkov, 2003). See the ‘Sukachev’s cross’ on Figure 4 for ecological characteristics of forest types.

development rather than its variation was the main interest. A chronosequence approach was used to determine the general developmental patterns and to construct growth tables for even-aged single-species stands, termed ‘natural normal’ stands. However, such stands were extremely difficult to find (Ilvessalo, 1937). In the 1950s the multiple pathways of forest regeneration and their association with various stand structural types were documented by Voropanov (1950) and Baranov and Grigoriev (1955).

A series of forestry studies traced the successional process leading to an uneven-aged stand structure. Alekseev (1948) published a scheme for the development of northern boreal (Arkhangelsk region) green-moss Norway spruce forests originating after a fire. This scheme suggests that strong competition between spruce and birch is observed in the young and middle-aged stands. By 80 years after the fire, spruce dominance is assured, the birch proportion is circa 30% and between 60 and 80 years the total mortality constitutes 30% out of the initial standing volume. At ages of 100–120 years the competition increases and the total mortality amounts to 10.0–11.6% of the volume; the basal area thus increases. The period of high mortality (14–16%) begins at 140 years and lasts about 120 years. The basal area constantly decreases (by 56% from 120 to 240 years). After 240 years the stand die-off (Zerfallphase, according to Leibundgut, 1982) is catastrophically rapid: the mortality amounts to 52% and the basal area falls significantly. The first generation disappears by 300–320 years after the fire. An uneven-aged stand with an annual volume increment of about 0.25% gradually forms (Alekseev 1948). Voropanov (1950) presented a similar scheme in more detail and pointed out the time of appearance and dynamics of each generation.

Kazimirov (1971) suggested a similar scheme for endogenous development of Norway spruce forests in Karelia, southern Boreal Zone (Fig. 7), and supplemented it with numerical data on the dynamics of standing volume, density, mean age, diameter, height and volume increment. This scheme shows that the maximum stand volume is reached by circa 140 years, and then decreases until the regeneration of the second post-disturbance cohort. A “stable” (steady state) volume is achieved after 560 years of stand development. The lifetime of cohorts is circa 240 years. The tree number oscillates according to the establishment and die-off processes of the cohorts. Volume increment also oscillates, reaching a maximum at 80 years, collapses then at 220 years, increases again and then gradually stabilizes (Kazimirov, 1971).

In northern Finland, Sirén (1955) studied Norway spruce forests at moist *Hylocomium-Myrtillosum* sites and divided their postfire development into two main stages: “primary”, denoting the development after a fire, and “secondary”, which is initiated after the “collapse” of the first spruce cohort (Fig. 8). Sirén’s (1955) data show a pronounced strong wave-like pattern with a drastic drop of the living stand volume after 300+ years of succession. It is noteworthy that such a strong wave pattern has not been reported elsewhere (cf. Dyrenkov, 1984). The drastic developmental pattern proposed by Sirén may have been influenced by subjective sampling and the relatively small size of the sample plots (Sirén, 1955; p. 37–39).

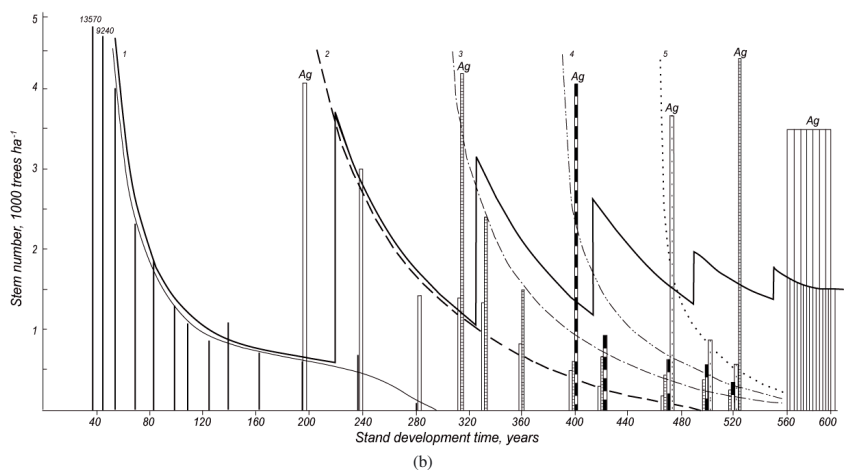
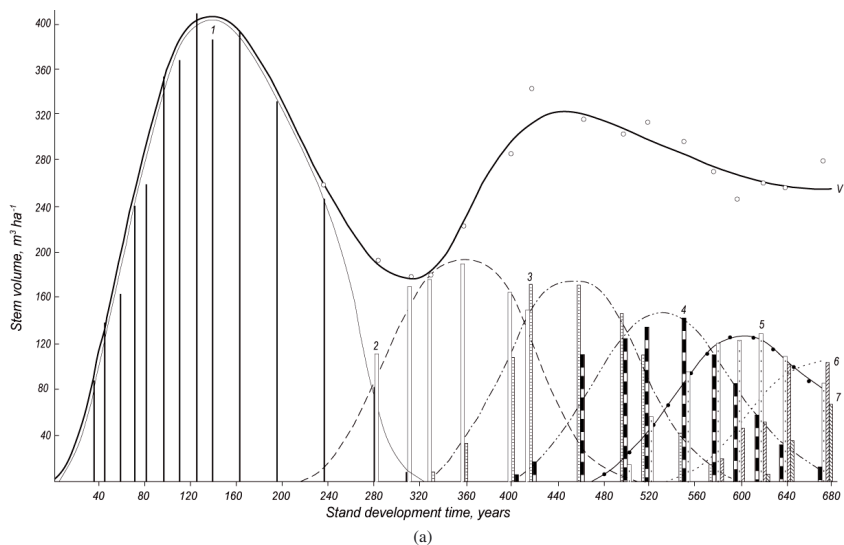


Figure 7. Dynamics of (a) standing volume, (b) stem number and (c) volume increment of a Norway spruce (*Picea abies*) stand in *Piceetum myrtillosum* (medium fertility and moisture) forest type in Karelia (redrawn from Kazimirov, 1971). 1–7: Numbers of cohorts, circles: empirical data from sample plots, solid lines: theoretical curves, Ag: seedlings and undergrowth.

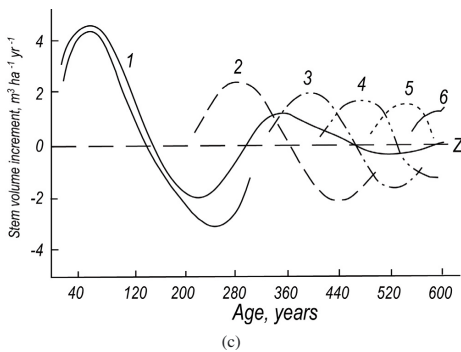


Figure 7. Continued

In Sirén's (1955) scheme birch is the first dominant in the "primary" succession, but spruce acquires dominance circa 80 years after the fire (Fig. 8). At 240 years after the fire, almost pure spruce stands attain the maximum standing volume of circa 280 m³/ha. The stand die-off occurs by circa 360 years, leading to natural regeneration of spruce and birch. This is the start of "secondary" succession, according to Sirén (1955), but this time spruce is dominant from the beginning. In 220–240 years a new but lower peak of standing volume is attained at circa 190 m³/ha. The main reason for the declining productivity according to Sirén (1955) is the accumulation of raw humus and the consequent immobilization and slow cycling of nutrients.

In the northern boreal forest in Russia, Dyrenkov (1984) observed a productivity decline in fire-originated spruce forests with successional development, but he stated that it is not a widespread phenomenon. In contrast, he reported stand characteristics in late successional spruce forests to be stable.

Schemes for endogenous development were also constructed for Siberian and Far-Eastern mixed dark coniferous forests. Falaleev (1985) suggested that the dark coniferous Siberian forests gradually pass through a 7-stage cycle from young to over-mature forest and then final die-off. This endogenous development could be interrupted by human-induced (clear-cuttings) or natural (fires, insect outbreaks, windthrows etc.) disturbances. Man'ko (1967), in studying the spruce-fir forests in the Far East, distinguished the following developmental phases: (1) maturity, (2) overmaturity of the dominant spruce generation, (3) the temporal dominance of fir and (4) forming the new forest stand dominated by spruce. Komin (1983) and Kozin (1982), working in the Russian Far East, suggested a scheme of cyclic endogenous successional development in uneven-aged virgin forest associated with solar activity. Komin (2003) argued that endogenous development of forest stands requires 1 000–1 200 years to attain an all-aged state with fine-scale gap dynamics. Most stand development sequences in the Urals and Siberia include tree species replacement (Kataeva and Korzukhin, 1987; Konstantinov and

Gorozhankina, 1995; Smolonogov, 1968; 1990). The schemes of postfire dynamics of Siberian pine forests constructed by Smolonogov et al. (1971), Kostuychenko (1977; see Kataeva and Korzukhin, 1987), Sedykh (1979), Smolonogov (1990), Furyaev (1996) and Pakhuchij (1999) represent successional variants in which shade-tolerant Siberian pine outcompetes the birch, aspen, spruce, and fir, and finally predominates.

Interesting zonal and site-specific peculiarities of post-fire dynamics of polydominant dark coniferous forests in the Western Siberian Plain were described by Smolonogov (1990) (Fig. 9). In low-density tree communities in the sub-tundra, characterized by extremely dry and poor growth conditions (*vaccinoso-ledosum* type), Siberian pine predominates throughout the 300–350 years of stand development, i.e. until die-off of the first postfire cohort. Siberian pine recruitment is abundant at the initial stages of succession together with silver and downy birch and spruce. In the northern Boreal Zone, birch with an admixture of aspen predominates at the initial stages in the same *vaccinoso-ledosum* forest type, however, Siberian pine and Scots pine also regenerate. Siberian pine together with other coniferous species acquires dominance by 60–80 years after the fire (Smolonogov, 1990). In the middle Boreal Zone, e.g. in the *hylocomiosum* forest type with average moisture and productivity, the dominance of birch and aspen lasts until 80 years after the fire. Spruce and fir become dominant 80 years after the fire and remain dominant until 160 years after the fire. Increased mortality of the first post-fire cohorts of fir and abundant recruitment of the next cohorts of Siberian pine, spruce and fir begin from 160 years and last until 400 years after the fire.

Under optimal conditions in the southern Boreal Zone (e.g. *hylocomiosum* forest type, average moisture and productivity) the dominance of deciduous tree species lasts approximately 100 years, after which spruce predominates until 180 years with a high proportion of fir. The period 180–400 years after the fire is characterized by the dominant role of Siberian pine with a high admixture of spruce and fir at the beginning and their dominance at the end of the period. All the species form several cohorts during succession. Siberian pine under these optimal conditions rarely forms the next postfire cohorts, which can be explained by its sometimes low seed production, rodents feeding on seeds, intense competition with spruce and fir, as well as by vigorous grass cover in gaps. The dynamics of dark coniferous forests on gleysols (*filipenduloso-equisetosum*, *equisetosum-fruticulosum-sphagnosum* forest types) is different. These forests burn very seldom; consequently it is almost impossible to find stands younger than 80 years. All processes are gradual. Birch can predominate until 100 years but does not form a separate layer. Siberian pine forms several cohorts, while the percentage of spruce, fir and pine is stable throughout succession (Smolonogov, 1990).

Dyrenkov (1984) suggested five main types of Eurasian boreal spruce forest dynamics. The first dynamic type represents the 400–600 year postdisturbance development from stand-replacing disturbance to an all-aged stand. The second type, "oscillation dynamics", is associated with medium-severity disturbances, e.g. windthrows, in those stands which had been close to an all-aged structure. The cycle lasts 150–200 years.

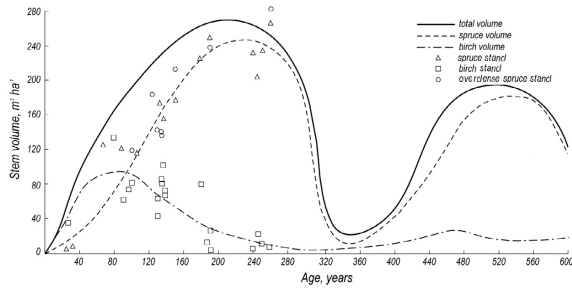


Figure 8. Development of stem volume ($m^3 ha^{-1}$) of spruce and birch after fire in the northern *Hylocomium-Myrtilus* forests in Finland according to Sirén (1955). The 600-years development consists of two wave-like phases, in Sirén’s terminology the ‘primary’ and ‘secondary’ successions. The data points are available only for the former one. The figure was redrawn from Sirén’s (1955) figures 24 and 27.

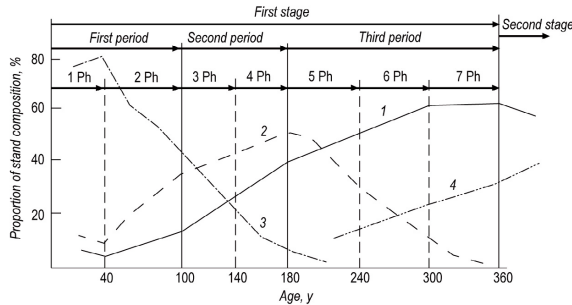


Figure 9. Successional development of green-moss-herb Siberian pine forest stand. 1: Siberian pine (*Pinus sibirica*), 2: Siberian spruce (*Picea obovata*) and fir (*Abies sibirica*), 3: deciduous species: birch (*Betula pubescens*, *B. verrucosa*, *B. krylovi*) and aspen (*Populus tremula*), 4: new cohorts for spruce, fir and Siberian pine, Ph: phase. The figure was redrawn from Smolonogov (1990).

The third dynamic type, “die-off – regeneration”, is associated with “nonsignificant” destruction of all-aged stands lasting several decades. The fourth type, “uneven, wave-like regeneration process in pristine spruce forests”, is associated with periodical disturbances. The cycle lasts from several decades to 100–150 years depending on the severity of disturbances. Dyrenkov (1984) showed that this fourth type, which in modern understanding can be called cohort dynamics (Angelstam and Kuuluvainen, 2004) predominates in most boreal forests. Finally, the fifth type in Dyrenkov’s system is an “even regeneration process of all-aged stands” (fine-scale gap dynamics). According to Dyrenkov (1984), the changes in tree species composition between *Picea* ↔ *Betula*, *Populus* and *Tilia* can occur only in the first and second dynamic types, the changes in *Picea* ↔ *Pinus* can occur only in the second type, while *Picea* ↔ *Abies*, *Pinus sibirica* can occur in the second, third and fourth types during successions in polydominant coniferous stands.

The above examples illustrate that several classification schemes were developed to describe the dynamics of dark

coniferous taiga, i.e. forests dominated by Norway spruce, or Siberian spruce, fir or pine. In general, two main dynamic types were described: (1) endogenous stand development leading to formation of the uneven-aged or all-aged stand structure associated with small-scale dynamics, stabilization of volume and increment and, in some studies, concurrent with a gradual change in site conditions, and (2) dynamics associated mainly with more severe and larger-scale disturbances. This distinction provided a framework for later studies.

4.2.2. Light coniferous taiga

The dynamics of the light coniferous forests, i.e. shade-intolerant such as Scots pine and larch, are usually associated with concurrent low-intensity fires. However, nonpyrogenic endogenous successions of Scots pine forests have been described as well (Zyabchenko, 1970).

Zyabchenko (1984) suggested a scheme for endogenous development of Scots pine forest based on empirical data

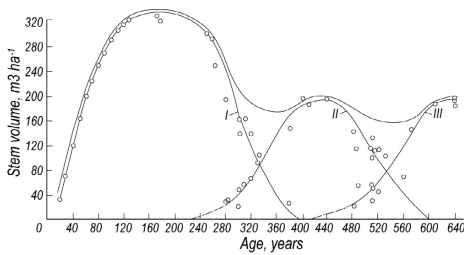


Figure 10. Dynamics of the standing volume of Scots pine (*Pinus sylvestris*) (*Pinetum vacciniosum*, dry and poor forest type) stand in Karelia and Murmansk region based on 53 sample plots. I, II, III – cohorts. The figure was redrawn from Zybchenko (1984).

acquired from the Kola Peninsula, Murmansk region and Karelia (Fig. 10). The succession begins from open areas (burned areas, clearcuts) colonized by pine and is completed by mortality of the first tree generation and appearance of a new one from advanced regeneration. Usually this occurs at approximately 280 years of stand age, and by 400 years of stand age almost all the trees of the first generation have died. A feature of the first phase is the absence of a period of suppression by dominant trees. The stands are even-aged and characterized by high standing volume, high density and no pronounced vertical stratification. The time of entry of the second generation into the upper tree layer (at 280–300 years) corresponds to the second phase of development. This phase lasts until die-off of the second generation at 480–500 years. At this stage, the stands are uneven-aged, with at least two generations of trees, pronounced vertical structure and less standing volume, compared with the stands of the first phase. Most pines of the second generation remain suppressed for circa 80 years. After die-off of the second pine generation, the favourable conditions for regeneration of the third generation are developed. In approximately 600 years after colonization of open land, the uneven-aged stands are formed, with two or more age cohorts, or generations of trees, and with almost all trees having experienced a suppression period. At this time the third and final phase in endogenous development of a pine stand begins, resulting in a stand reaching the “climax” stage, according to Zybchenko (1984).

The process of endogenous forest development can be interrupted and reset back to the starting point by severe stand-replacing fires, whereas less intense surface fires create a cyclic regeneration pattern of fire-adapted tree species such as Scots pine and Siberian larch. The regeneration of the latter type of forests has a wavy-like character: the regeneration coincides with favourable conditions (seedbeds and canopy gaps) created by fires. Utkin (1965) went so far as to claim that there are no larch-dominated forests in central Yakutiya that have developed without fire. The cohort dynamics of larch forests due to periodic surface fires and cyclic dynamics of their age structure were verified by Glagolev (1975; 1976) and Shevelev (1999).

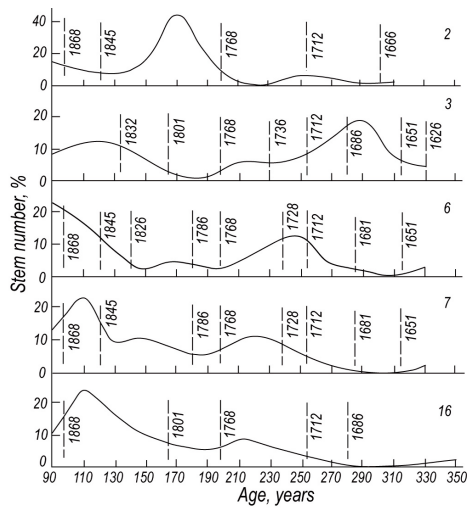


Figure 11. Age distribution of trees in uneven-aged Scots pine (*Pinus sylvestris*) forest stands in Russian Karelia with dated surface fires (shown with vertical dashed lines). 2, 3, 6, 7, 16 are numbers of the sample plots. The figure is redrawn from Zybchenko (1986).

Fire severity determines the subsequent successional dynamics: even-aged stands are formed after high-severity fires, while uneven-aged stands are formed by low-severity surface fire regimes. Zybchenko (1984) provided evidence for the higher proportion of uneven-aged stands under poorer site conditions than on more fertile sites; he also described a wave-like cohort dynamics induced by fire for pine forests in Karelia (Figs. 10 and 11).

Verkhunov (1979) described the development of Scots pine stands in Siberia. He distinguished the following developmental stages for each generation: (1) undergrowth initiation and stem exclusion, by 60 years; (2) mature forest, by 120 years; (3) transition from maturity to over-mature by 180 years; (4) old growth by 320 years and (5) very old growth and die-off. Verkhunov (1979) showed that each generation repeats this developmental scheme and associated the regeneration of each new pine cohort or generation with the occurrence of surface fire.

The successional stage of the stand affects the survival of trees in a fire and their subsequent successional development. Verkhunov (1970) described the fire – forest community interactions in Scots pine stands in Siberia, showing that trees younger than 30–40 years old die in the fire, and that the successional dynamics of these stands are interrupted. In older but pre-mature even-aged pine stands, high but spatially heterogeneous fire-induced mortality leads to appearance of gaps filled by regeneration of the next cohort. In mature even-aged stands, surface fires cause mortality of only suppressed small trees.

However, the poor light conditions do not allow the next cohort to establish. Finally, in overmature even-aged stands, fire kills not only small but also older weak trees. Thus, part of the old tree cohort dies off, opening space and stimulating recruitment of a new tree cohort. Subsequently, an uneven-aged stand is gradually formed. Surface fires occurring in uneven-aged stands create complex tree age structures. However, mortality of older trees and the subsequent recruitment of new ones are not abrupt events but gradual processes that broaden tree age distributions (Verkhunov, 1970).

In western Siberia, the types of Scots pine forest were ranked by Verkhunov (1970) in decreasing order of fire frequency and severity as follows: lichen, cowberry, green-moss-herb, long-moss and sphagnum sites. The highest degree of fire-induced uneven-agedness was observed in the lichen and cowberry types (Verkhunov, 1970). The reviewed studies indicate that in the light coniferous taiga surface fire is the central factor driving cohort dynamics and supporting complex uneven-aged stand structures in Scots pine and Siberian larch-dominated forests.

5. A SYNTHESIS OF STAND DYNAMICS

The studies reviewed demonstrate that the interrelationships between the forest-forming factors, mainly dominant tree species and site conditions together with associated disturbance regimes, lead to a wide range of natural variability in stand structures. Accordingly, multiple successional pathways in stand development have been demonstrated both in dark and light taiga forests. In general, all-aged stands are gradually formed over several hundreds of years of endogenous succession. This endogenous development can be interrupted by stand-replacing or partial disturbances, such as fires, windthrows and insect outbreaks.

Boreal forest dynamics can be classified according to time since disturbance, prevailing disturbance regime, site type and stand characteristics, into the following stand dynamic types:

1. Even-aged, compositional change development,
2. Even-aged, mono-dominant development,
3. Cohort dynamics,
4. Fine-scale gap dynamics.

These stand dynamic types are related to certain site conditions, age and diameter distribution, dominant species, severity of disturbance, time since last disturbance, and spatial structure (Tab. 1). Even-aged dynamics (types 1 and 2, Tab. 1) are pronounced after stand-replacing disturbances such as fires, windthrows and insect outbreaks. The more nutrient-rich the site conditions, the higher is the probability of type 1, with a more pronounced dominant role of deciduous tree species (birch, aspen) in early succession after disturbance, and the longer is the delay in achieving the dominance of coniferous tree species (spruce, fir). In stand dynamic type 1, the replacement of tree species lasts from 60 up to 180–200 years. The mechanism of development may vary depending on the size and decline age of short-living hardwoods in the stand composition. This dynamic type represents a mechanism of replace-

ment of light taiga by dark taiga in the absence of fire and back e.g. in case of recurrent surface fires.

Mono-dominant development (type 2) occurs on poor sites where a single tree species is a superior competitor, such as Scots pine on dry heaths (Aaltonen, 1919) and spruce in poorly drained spruce forests (Fedorchuk et al., 1998).

In both stand dynamic types 1 and 2, successional development may be interrupted by disturbance. However, in the absence of disturbance and with senescence of the trees from the initial cohort, canopy gaps are gradually formed, leading to a patchy recruitment of new cohorts and the stand shifts first to type 3 dynamics and then gradually, if free from major disturbances, over lengthy periods, toward type 4 dynamics characterized by all-aged forests. In dynamic type 2, this process requires significantly more time than type 1.

Cohort dynamics (type 3) prevail when recurring partial disturbances stimulate cyclic regeneration processes and lead to a multimodal stand age structure (Tab. 1). In cohort dynamics different phases can be distinguished: a regeneration phase, a phase of growing stock increment (young cohorts predominate), stabilization and growing stock decline (old cohorts predominate) (Fedorchuk et al., 1998). The oscillation of these phases is dependent on the disturbance type and severity that influence regeneration conditions: from decades in the case of mid-severity windthrow to centuries in the case of stand decline due to insect attack, e.g., by the Siberian silk moth.

Fedorchuk et al. (1998) showed that when a stand has escaped exogenous disturbances for lengthy periods, the pronounced oscillations in tree mortality and regeneration are dampened, and the stand dynamics become characterized by a fine-scale mosaic of stochastic mortality and regeneration processes. This is type 4 dynamics, in which the stand can be considered to be in "quasi-equilibrium" and all tree age classes are continuously present. These late-successional stands are not necessarily monodominant. Usually the percentage of deciduous trees increases with increase in site productivity (Pugachevsky, 1992).

The endogenous process of transition from the first or second to fourth types of dynamics can last for centuries. Based on studies of the chronosequence of forest ecosystems, Kazimirov (1971) (Fig. 6) in Russian Karelia, middle Boreal Zone and Pugachevsky (1992) in the Tver region (the Central Biosphere Forest Reserve, southern Boreal Zone) concluded that formation of all-aged Norway spruce stands after a stand-replacing disturbance could require 600–700 years, depending on site conditions.

6. MANAGEMENT IMPLICATIONS

We conclude that if the aim is to manage the forest to maintain its ecological characteristics it is necessary to take into account the high diversity of stand structures and developmental pathways naturally occurring in Eurasian boreal forests. Interestingly enough, leading Russian forest scientists in the early 20th century already warned against searching for a single universal silvicultural method (Bogushevsky, 1912; Morozov, 1925; Tkachenko, 1931; Yashnov, 1934). They emphasized that the forest represents a geographic phenomenon

Table 1. Characteristics of the main types of forest dynamics under natural disturbance regimes.

Type of stand dynamics	Characteristic site conditions	Age structure type* / Tree diameter distributions	Dominant tree species	Time since last stand-replacing disturbance / Possible transitions to other types of dynamics	Driving factors, processes	Spatial structure, size of gaps / vertical structure	References
1. Even-aged, compositional change development	Medium to high productivity, well drained	1 / Unimodal or two peaks	Western Europe: <i>Betula</i> sp., <i>Populus tremula</i> , <i>Tilia cordata</i> , <i>Pinus sylvestris</i> → <i>Picea abies</i> Eastern Europe, Siberia: <i>Betula</i> sp., <i>Populus tremula</i> , <i>Pinus sylvestris</i> , <i>Larix</i> sp. → <i>Picea obovata</i> , <i>Abies sibirica</i> , <i>Pinus sibirica</i>	60–180 / 3, 4	Initial stand-replacing disturbances: fires, windthrows in Europe, fires, insect outbreaks in Siberia → endogenous dynamics	Patchy, gaps < 0.2 ha / 2 layers	Sirin, 1955; Dyrenkov, 1984; Smolnogo, 1990; Fedorchuk et al., 1998
2. Even-aged, mono-dominant development	Low and medium moisture and productivity	1 / Unimodal	All tree species; no compositional change	0–180 / 3, 4	Initial stand-replacing disturbances: fires, windthrows in Europe, fires, insect outbreaks in Siberia → endogenous dynamics	Even, gaps < 0.2 ha / one layer	Voropanov, 1950; Baramov, Grigoriev, 1955; Sirin, 1955; Dyrenkov, 1984
3. Cohort dynamics	All site conditions in fire-driven communities; medium to high moisture and productivity in windthrow-driven communities	3 / Multimodal	Western Europe: <i>Picea abies</i> , <i>Pinus sylvestris</i> Eastern Europe, Siberia: <i>Pinus sylvestris</i> , <i>Larix</i> sp.; <i>Picea obovata</i> , <i>Abies sibirica</i> , <i>Pinus sibirica</i>	> 180 / 4	Western Europe: windthrows, surface fires, fluctuations in moisture regime Eastern Europe, Siberia: surface fires, insect outbreaks	Patchy, gaps 0.1–0.5 ha / few layers	Aaltonen, 1919; Utkin, 1965; Verkhunov, 1970; Giagolev, 1975, 1976; Dyrenkov, 1984; Zyabchenko, 1984; Fedorchuk et al., 1998; Shevelev, 1999
4. Fine-scale gap dynamics	Low and medium moisture and productivity	2 / Reverse-J	Western Europe: <i>Picea abies</i> or <i>Pinus sylvestris</i> only in the driest or very moist poor site conditions Eastern Europe, Siberia: <i>Pinus sibirica</i> , <i>Picea obovata</i> , <i>Abies sibirica</i> , <i>Larix</i> sp., <i>Pinus sylvestris</i>	> 500 / 1, 2, 3	Endogenous dynamics	Mosaic, gaps < 0.2 ha / no layers can be distinguished	Bogushevsky, 1912; Ivashkevich, 1915; Semander, 1936; Skvortsova et al., 1983; Dyrenkov, 1984; Hytteborn and Packham, 1985; Smolnogo, 1990; Leemans, 1991; Liu and Hytteborn, 1991; Hojgaard, 1993; Fureyev, 1996; Kuuluvainen et al., 1998; Fedorchuk et al., 1998; Volkov, 2003

* According to Figure 3.

and that the choice of management method should be based on economic and ecological conditions as well as on the natural characteristics of forest stands. Similarly, in Finland Kalela (1948) emphasized that natural stand structures and developmental processes should form the basis for silviculture. Recently, reintroducing the selective system and other uneven-aged silvicultural systems back to forestry has been suggested and widely discussed in Scandinavian countries and Russia as important tools for sustainable forestry (e.g. Angelstam, 1998; Kuuluvainen, 2002; Lähde et al., 1999; Volkov, 2003).

Ecological forestry can be developed, based on the existing knowledge of natural stand structures and dynamics, such as the classification of stand dynamics presented in Table I (see also Angelstam, 1998; Angelstam and Kuuluvainen, 2004; Bergeron et al., 2002). For landscape-level forest management, it is important first to estimate the natural proportions of different stand dynamics types. Then, for each type, taking into account tree species composition and site conditions, silvicultural methods that match the natural dynamics can be applied (Dyrenkov and Shergol'd, 1973; Kangur et al., 2005; Pobedinsky, 1980; Tikhonov and Zyabchenko, 1990).

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ORIGINAL ARTICLE

A conceptual model of forest stand development based on permanent sample-plot data in Estonia

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Abstract

Ecosystem management assumes that management practices based on natural disturbance patterns are likely to preserve both natural biodiversity and ecosystem functions. Ecosystem management thus combines traditional natural resource management and forestry practices together with classical notions of protection that are focused on sustaining a naturally evolving ecosystem. Increased knowledge and understanding of natural disturbance dynamics in boreal forest ecosystems allow for the creation of a template for sustainable forest management that is based on mimicking disturbances that are thought to contribute to the biodiversity of the ecosystem. The observed trends of natural development are discussed in this paper. Permanent sample-plot data are used to develop a conceptual model of stand succession following natural disturbance. The distinctive characteristics of disturbances that are relevant to forest management planning are identified and modelled.

Keywords: *Forest management, natural disturbances, permanent plots.*

Introduction

Management actions that attempt to approximate natural disturbance regimens need to mimic the temporal and spatial patterns generated by the life cycles of the different plant species. These management practices must be rationalized with studies concerning both the natural and artificial factors that affect the ecosystem dynamics.

The disturbance factors that contribute to the dynamics of boreal forest ecosystems are a complex combination of natural factors such as wind, fire, animals, insects and pathogens, together with the anthropogenic influences of management, recreation and pollution (Barreñada Sanz, 2001; Kuuluvainen, 2002a). Disturbances, whether natural or anthropogenic, affect forest structure, composition and ecological processes on a wide range of spatial and temporal scales and on all levels of ecological organization (Stanturf, 2004; Kangur et al., 2004).

The recognition among foresters, forest managers and forest scientists of the important role of natural disturbances to meet the growing and changing

demands on forest goods and services has created a need for comprehensive scientific knowledge about natural disturbance dynamics and its effects on forest ecosystem dynamics (Kuuluvainen, 2002b; Vodde, 2002; Kangur et al., 2004).

Studies on the long-term vegetation dynamics are often conducted using chronosequences (Brubaker, 1981). A contrasting approach is to monitor permanent sample plots. The data gathered from long-term studies, including both observational and experimental investigations, can be used to formulate hypotheses on the mechanisms of species replacement during various successional stages. Chronosequences generally contain unexplained variation components (Bakker et al., 1996). In this paper the permanent growth and yield sample-plot data are used to develop a conceptual model that describes and can be used to analyse the stand development processes on fresh boreal forest type (*Oxalis* and *Oxalis-Vaccinium myrtillus* site type) (Paal, 1997) in Estonia.

Stand development phases are discussed in several classic works (Bromann & Likens, 1979; Oliver &

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Larson, 1990; Frelich, 2002). The main aim of this study was to analyse forest stand development on the permanent sample plots. The four basic stages of stand development described by Frelich (2002) are discussed and conceptualized. The concept of mimicking natural disturbances with applicable cutting regimens is presented.

Materials and methods

Sample area

The modelling area for disturbance analysis was the Järvselja Training and Experimental Forest District. The sample area was selected in the Järvselja Experimental Forest of the Estonian Agricultural University (58°16' N, 27°118' E).

Data from 37 permanent sample plots were used to calibrate the theoretical development trend of the stand. Data from 18 permanent sample plots where Scots pine (*Pinus sylvestris* L.) was the dominant tree species were used for analysing stand development processes on fresh boreal forest type. These permanent forest growth and yield monitoring plots were established from 1925 to 1935. On average, there have been nine measurements for each plot from 1925 to 2004. The average-sized plot is 0.12 ha. Scots pine was the dominant tree species on 30 plots, birch (*Betula pendula* Roth) on three plots and Norway spruce [*Picea abies* (L.) Karst.] on four plots. The average stand age in 2004 on Scots pine-dominated plots was 126 years, birch-dominated 107 years and Norway spruce-dominated 104 years. The stand age varies between 73 and 203 years.

The plots were rectangular and distributed all over the modelling area. The small size of the plots was compensated for by using a high number of replicates inside each stand. All stands have been managed, but only partial records of the detailed management regimens are available for some of the sites (mainly 10–15 years after the establishment of the plot). The main natural disturbance factor in Järvselja forests is wind. Fire has not naturally been a major factor for forest in Järvselja.

Calculations and data analyses

The gradual shift in stand structure and composition was characterized by the change in stand mean diameter, volume and stand density.

The stand mean diameter development trend was constructed. Individual live tree volume was generated using the volume functions of Laasasenaho (1982), which are based on diameter at breast height. For *Pinus* and *Larix* species the functions for Scots pine were used, for *Picea* and *Abies* species

the functions for Norway spruce were used, and for all deciduous tree species the function for birch was applied.

The diameter and volume development series were compared with the difference models of Kiviste (1999a, b). Kiviste's (1999a, b) models have been developed on the basis of 206 Estonian state forest districts forest inventory data from the 1984–1993 inventory period. The models were fitted with a presumed maximum stand age for each series corresponding to the optimal rotation period of the dominant tree species (pine 120, spruce 100, birch 70, aspen 60, alder 50, ash and oak 120 years). Since the Hossfeld growth function, which is the basis of the model, corresponds in general to natural stand development principles, the models are expected to predict reliably the height, diameter and volume values in older aged stands. Kiviste's (1999a, b) models are used to represent the average diameter, volume and height values of Estonian forests on the fresh boreal forest type and are compared with the Järvselja permanent sample-plot data.

The tree size data were combined with stand density. The optimal stand density trend was characterized using Kiviste's (1991) function (1) of optimal stand density between the number of trees in a stand and stand mean diameter for pure pine stands:

$$100/N^{0.5} = -0.033 + 0.00928 \cdot H_{100} + (0.195 - 0.0022 \cdot H_{100}) \cdot D \quad (1)$$

where N = trees per hectare, D = stand mean diameter (cm) and H_{100} = stand height at the age of 100 years.

Theoretical model of forest successional cycles

The main factors affecting the windthrow gap formation are tree size and position. Figure 1 is a generalization of many similar successional cycle descriptions. The predisturbance state is an important factor in the ensuing stand's development. In this model the structure of the predisturbance stand is described in two groups. The first group, regular stands, has an even-aged and even-sized stand structure. The second group, irregular stands, has developed from regular stands and small disturbances. The resulting structure, based on gap dynamics, contains trees that are uneven aged and uneven sized.

Four basic stages of stand development

The four basic stages described by Frelich (2002) were modified (Figure 2) to fit the theoretical

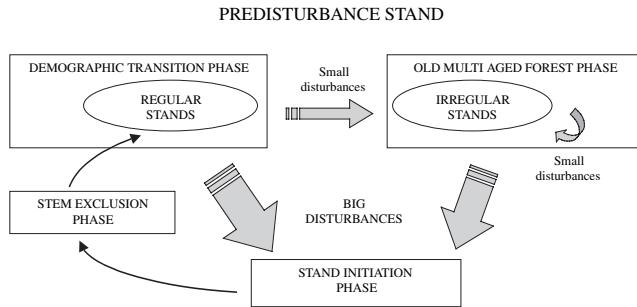


Figure 1. Theoretical model of forest ecosystem successional cycles (Vodde et al., 2002) following disturbances by wind and storm on stands in different stages of stand development (Frelich, 2002).

development trend of tree stands on a fresh boreal forest type after a stand-replacing disturbance. The effect of intensive management on the forest stand structure and composition produces a marked distinction between unmanaged and managed stands (Kuuluvainen et al., 2002; Rouvinen & Kuuluvainen, 2004; Kangur et al., 2004).

The stand initiation stage (1) follows a major disturbance. This disturbance can be natural (stand-levelling storm, crown fire, insect or fungus attack) or anthropogenic (clear-cut logging). This initiation stage lasts from the stand-replacing disturbance until the continuous canopy forms and trees begin competing with each other for light and canopy space. During the stem exclusion stage (2), the canopy is dense enough to prevent new saplings from growing into the canopy. The stem exclusion stage lasts until the tree canopy is dense enough to induce a density-dependent self-thinning mortality in the stand. The demographic transition phase (3) is characterized by a heterogeneous stand structure with, in particular, an irregular spacing (Kuuluvainen, 2002b). The understorey establishment in this stage is an essential component for the shift to an old, multiaged stand. During the old, multiaged phase (4), the understorey formation is a characteristic, site-specific process (Rebane, 1969; Jögiste & Vää, 2002).

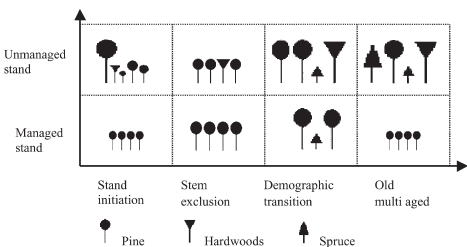


Figure 2. Successional developments of forest stand on fresh boreal forest type.

Results and discussion

Stand characteristics

The stand disturbance history can be deduced from tree-ring data (Frelich, 2002). The increment can reveal both catastrophic destruction of the main canopy and minor changes in the lower canopy. Permanent sample-plot data from remeasurements provide a method to study stand dynamics using explanatory variables to generate the incremental changes. These climate and stand level variables can be used in process-based models.

Table I summarizes the basic characteristics of the permanent sample plots. Figure 3 provides an illustrative example from the permanent sample-plot data following the timeline from the establishment of the plot. Gradual increases in the mean diameter on the sample plot were observed.

In Figure 4, the decreasing trend in the rate of increase in stand mean diameter with respect to age can be seen. On fresh boreal forest types in pine-dominated stands the Järvelja permanent sample-plot data compared with Kiviste’s (1999a, b) model for the Estonian average indicate lower stand mean diameter values in older stands. The differences in stand mean diameter distribution in older stands compared with Kiviste’s model can be related to less intensive forest management in the Järvelja forests. The demographic transition phase creates stands that have older trees together with small diameter, younger trees. The average diameter of these mixed

Table I. Characteristics of permanent sample plots in Järvelja.

	Birch	Spruce	Pine
No. of plots	3	4	30
Mean age	107	104	126
Mean height (m)	23	25	21
Mean diameter (cm)	26	26	23

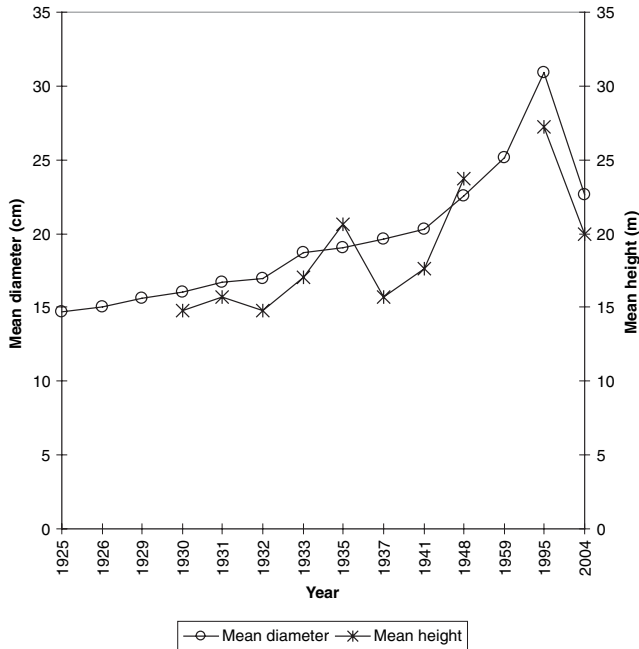


Figure 3. Example from the permanent sample-plot data following the timeline from the establishment of the plot.

stands will be lower than that of the even-aged managed stands represented by the model.

The permanent plot data in Figure 5 indicate that there is still a considerable volume increase in stands that are over 100 years old. There is a perceivable level of net ecosystem productivity in these old stands (Peet, 1992). The gradual increase in volume exceeds considerably the Kiviste (1999a, b) model's average prediction. It suggests that the net productivity can be high in old stands. The total productivity can be only slightly higher because the intermediate cuttings have been mild.

On observed sample plots surprisingly high stand density (Figures 6 and 7) could be detected during the whole study period. In Figure 6 the decrease in stand density with time is presented by each individual sample-plot series. Figure 6 also shows the distribution of initial ages for the study plots at the time of establishment. The study plots represent two age groups: stands less than 100 and stands between 100 and 200 years old. In both time-series groups there has been a noticeable increase in stand density during the past few decades. At the same time, stand mean diameter values are declining (Figure 4). These two phenomena can be related to two different aspects of stand development. Stands in the younger time-series group undergo the develop-

ment of a stem exclusion stage and reach the phase of demographic transition, and stands in the older time-series group undergo the development of a demographic transition stage and reach the phase of old multiage forest (Frelich, 2002).

The length of the stand development phases depends on the site type. The rate of stand development is highly dependent on site quality, whereas size-density relations of the stand are independent of site quality (Long et al., 2004).

The stand management and density relationship can be followed in Figure 7. In the case of managed stands a density diameter relationship follows the stand optimal density curve but hardly crosses it. Since the establishment of the permanent sample plots these forests have only experienced low-intensity management, except for two plots where strong precommercial thinning has been carried out. The cuttings were very mild, mainly involving the removal of dead or dying trees. This management regimen has led these forests into the situation today, where there is a large variation in stand structure and stand composition. In this sense, the cutting regimen has reflected (mimicked) the natural development of the stands.

Järvselja forests are generally regenerated after a wind disturbance (Kasesalu, 1993; Sepp & Rooma,

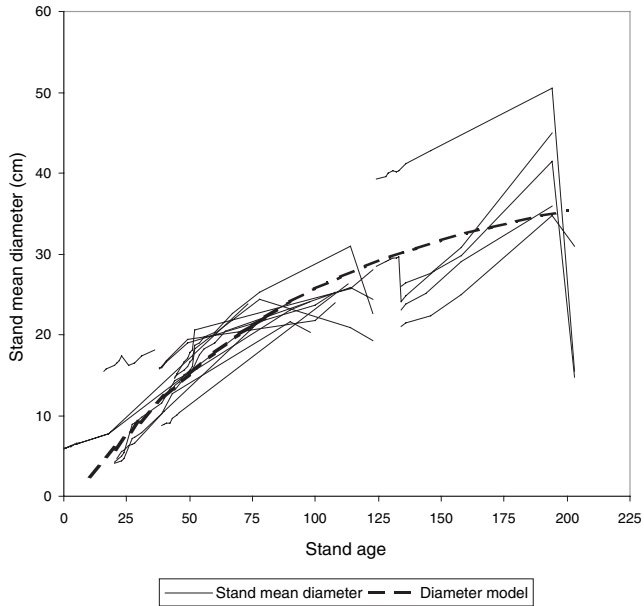


Figure 4. Pine-dominated stands mean diameter development trajectories on permanent sample plots in Järvelja compared with Kiviste's model (Estonian average) for pine on fresh boreal forest type.

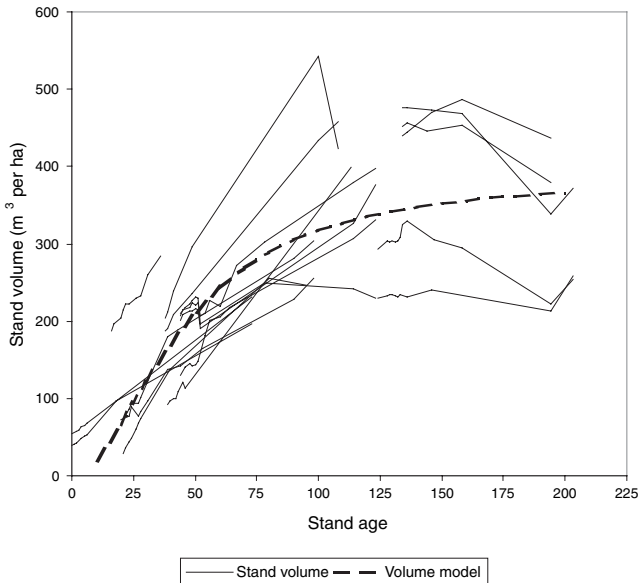


Figure 5. Pine-dominated stand volume development trajectories on permanent sample plots in Järvelja in comparison with Kiviste's model (Estonian average) for pine on fresh boreal forest type.

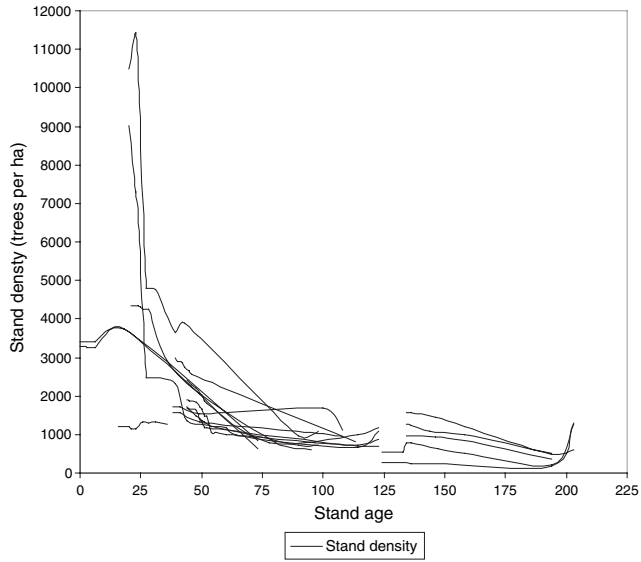


Figure 6. Stand density development trend on pine-dominated stands on fresh boreal forest type based on permanent sample-plot data.

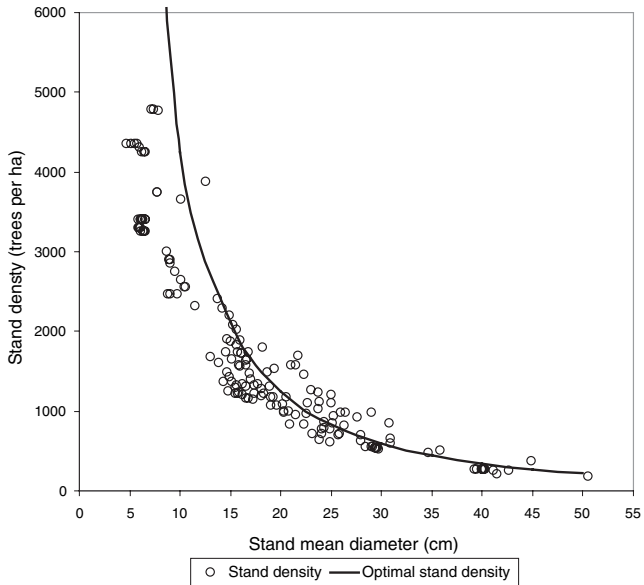


Figure 7. Relationship between stand mean diameter and stand density on pine-dominated stands on fresh boreal forest type based on permanent sample-plot data. The optimal stand density for Estonian pine stands according to Kiviste's model (1991) ($H_{100} = 30$ m) is shown with the continuous curve.

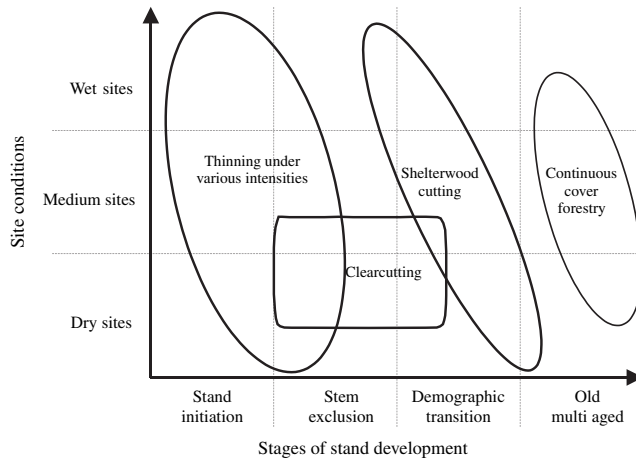


Figure 8. Outlying concept (based on sample-plot data) of mimicking natural disturbances with applicable cutting regimes.

1993). In this context, the term disturbance indicates a heavy loss of live biomass and is usually followed by a rapid biomass accumulation in growth processes.

Management implications

The theoretical trends of stand dynamics are presented in Figure 8. The ellipses in Figure 8 are tilted to show the centre of location of cutting regimens. The postdisturbance development leads to the mixed, multilayered stands. The forestry operations simplify the stand development. Precommercial and intermediate thinnings are the main silvicultural operations mimicking natural processes during stand initiation and stem exclusion phases. On dry and fresh sites clear-cuttings could simulate heavy natural disturbances in certain cases. On naturally developing stands on wet sites heavy natural disturbances hardly ever occur. Shelterwood cuttings can influence the demographic transition stage and on specific sites clear-cutting could be used. On clear-cuts some trees and tree groups should be retained to result in disturbance that feels more natural. Continuous cover forestry with low-intensity selective cuttings is the most suitable mimic of natural disturbance patterns during the old multi-aged stage.

Conclusions

The existing conceptual models can be matched with the real stand development trends in Estonian forests. The stand structural indicators indicate a high production capacity in late successional stages

of stand development. The investigation and measurement of regeneration establishment are of critical importance to models. Future work will concentrate on sampling young trees to follow the probable shift in stand composition.

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Tracking Disturbance-induced Changes in Stand Development at Irregular Measurement Intervals in the Järvelja Forest Experiments

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Abstract

Long-term sample plots have been used to study pathways of succession, and its mechanisms and causes. These observations are relevant not only to communities protected from human interference, but also to managed forests, where the objective is to explain response patterns following specific harvesting operations. The establishment and maintenance of a series of permanent plots requires a firm commitment beyond short-term economic fluctuations and political changes; nevertheless, such long-term experiments may be abandoned prematurely because of a lack of funding or changing policies. One aspect which has received little attention in the past is the “revival” of previously abandoned field plots. This paper analyses data from the Järvelja long-term forest experimental field plots which were abandoned in 1959 and “revived” in 1995 and 2004. This study distinguishes between two kinds of disturbance: natural and anthropogenic. The impacts of both kinds of disturbance are evaluated in terms of weight (quantity of biomass) and type (relative size of outgoing trees). Finally, the study evaluates density-dependent mortality or *self-thinning* using Reineke’s limiting line and Nilson’s stand sparsity. Our analysis found Nilson’s approach better suited for interpreting the limiting relationship in mixed forests and for estimating maximum density for different stand and site types; therefore, this topic will be pursued in future studies based on the extensive database of the Estonian Forest Research Plots Network.

Key words: long-term forest experiments, measurement gap, Reineke’s limiting line, Nilson’s stand sparsity

Introduction

Sustainable management of forest resources is based on empirical research. The aim of the early field experiments was to measure timber yields at different stages of forest development (Schwappach 1890). Some of these experiments have been re-measured for over a century, even during times of war, providing valuable information on long-term developments. It is often postulated that permanent plots are required in studies of long-term vegetation dynamics (Bakker *et al.* 1996), which is an especially valid assumption in forest ecosystems with long-living tree communities.

Berry *et al.* (1998) state that “quick fixes” and “one-time efforts” are not very helpful in ecosystems research. They argue that piecemeal efforts do not provide the required information about long-term response. They provide arguments in favor of a continuous, long-term observational infrastructure supported by long-term policies, budgets and research perspectives.

The establishment and maintenance of a series of permanent plots requires a firm commitment beyond short-term economic fluctuations and political changes. Nevertheless, it may happen that experiments which were originally designed for long periods of time are prematurely abandoned because of a lack of funding or changing policies.

Today, forest science is based mostly on empirical data, which should be measured systematically. In Estonia, the Network of Estonian Forest Research Plots (Figure 1) was gradually formed during the past 20 years upon the initiative of several Estonian scientists. This network comprises several different long-term forest monitoring, research and experiment series: a) long-term growth and yield study plots in Järvelja (Kangur *et al.* 2005), b) thinning experiments in Järvelja (Tullus and Reisner 1998), c) a series of long-term afforestation plots on abandoned oil-shale quarries (Korjus *et al.* 2007), d) a series of forest restoration experiments, and e) the network of permanent sample plots for forest growth modelling in Estonia (Kiviste and Hordo 2003).

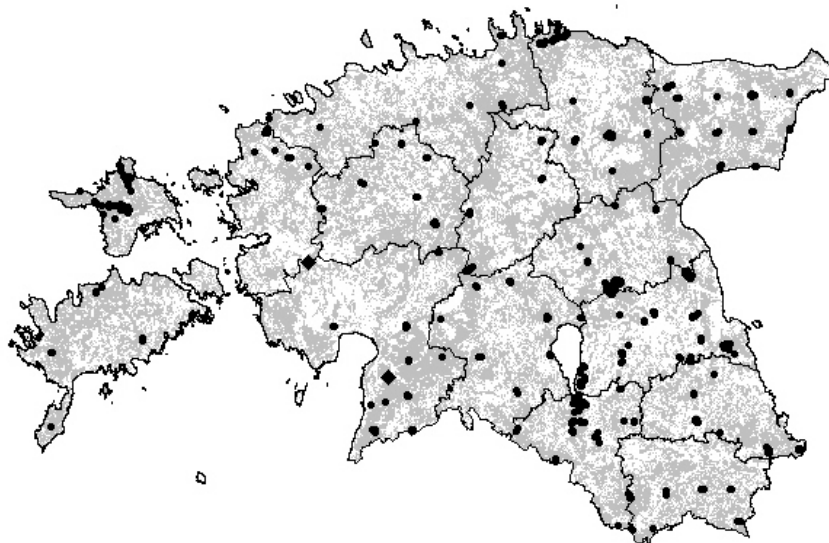


Figure 1. Map of Estonia showing the areas covered by forests (Peterson 2003) and locations of research plots

As an example, the Estonian Forest Research Plots Network currently contains 730 continually-re-measured permanent field plots for modelling forest growth. Table 1 shows the distribution of the plots according to site and forest types. The forest type is characterized by the dominant tree species. “Pine”, for example, refers to a forest where *Pinus sylvestris* either occurs as the only species or dominates by total volume. Such an infrastructure is often considered a national asset (Hasenauer 2006).

Table 1. Summary of the Estonian Forest Research plots, presented by group of types and dominant tree species (by volume)

Group of types	Pine	Spruce	Birch	Other	Total
<i>Full drained swamp forests</i>	13	11	11	0	35
<i>Meso-eutrophic forests</i>	28	94	12	1	135
<i>Alvar forests</i>	5	2	1	0	8
<i>Heath forests</i>	47	0	0	0	47
<i>Mesotrophic forests</i>	246	32	13	1	292
<i>Dwarf-shrub-sphagnum paludified forests</i>	7	1	0	0	8
<i>Grass fen forests</i>	0	0	7	0	7
<i>Nemoral forests</i>	0	30	54	43	127
<i>Bog moss forests</i>	13	0	0	0	13
<i>Herb-rich mixed forests on wet clay soils</i>	3	21	27	7	58
Total	362	191	125	52	730

Examples of forest experiments conducted over more than a century, providing an uninterrupted series of observations, are the extensive permanent networks maintained by a number of European forest research institutes (Hasenauer 2006). The extensive databases and data sets of different research series in the Estonian Forest Research Network have already provided scientists with much useful information, which has been presented at international conferences and published in international journals (Sims *et al.* 2006, Kangur *et al.* 2007). Nevertheless, the importance of combining data from earlier research series together with currently available materials is of high importance in long-term forest research.

One aspect which has received little attention is the use of previously abandoned field plots: Is it worthwhile to “revive” them and to continue with re-measurements after a long interval of abandonment? Missing data are a part of research. Data may be missing for several reasons, and there are alternative ways of dealing with these information gaps. When a previously abandoned experiment is re-established after a long time, the challenge is to make use of the entire period of observation, including the “observational gap”. In this

paper, we will propose ways of estimating the missing data for the entire development of the experimental plots.

Accordingly, the objective of this study is to present examples of such abandoned experiments with an estimate of the disturbance occurrence during the measurement gap and the potential forest density for an experiment with one species and two species. We will then show examples of previously abandoned experiments which have recently been re-measured.

Long-term experiments with irregular measurement intervals

Irregular measurement intervals in forest growth studies are quite common. They often occur when previously abandoned field plots are “revived”, *i.e.* re-measured after long periods of time during which no observations are available. When analysing disturbances for irregular measurement intervals, the observed time interval between re-measurements does not match the desired modelling interval. Thus, modelling annual tree growth and survival based on data with irregular measurement intervals requires specific interpolation of the independent variables during such “measurement gaps”, as demonstrated by Nord-Larsen (2006). Our study is not concerned with tree growth, however, but with recognizing forest disturbances during irregular measurement intervals.

Reviving old field experiments at Järvelja

The history of empirical forest research in Estonia can be traced back to the 19th century. Well-designed and -documented field experiments for forest research purposes were begun after the establishment of the Järvelja Forestry Training and Research Centre in 1921 (Mathiesen and Riisberg 1932). The Järvelja experimental forest is located in the South-Eastern region of Estonia near Lake Peipsi (at 58°16'N, 27°18'E).

Among the early long-term forest experimental series in Järvelja are growth and yield experiments initiated by Andres Mathiesen (Kasesalu 2003) and thinning experiments initiated by August Karu and Lembit Muiste (Tullus and Reisner 1998). Long-term forest growth and yield monitoring plots were established between 1922 and 1935. The rectangular experimental plots were relatively small, covering between 400 and 600 m². The small plot size was offset by a high number of replicates in the same stand. The experimental sites were selected such that all forest sites and dominant tree species in the

Järvselja region were represented. The basic stand parameters were measured and trees on the plots were numbered.

Originally, re-measurement intervals in the experimental areas were planned to range between five to ten years. However, because these areas were used in the field training of forestry students, they were re-measured more frequently during the first decade. The measurement data were stored in handwritten data journals and experiment case files. The last of these handwritten records dates back to 1959. Some of the plots were re-measured in 1977, 1984, and 1995, but for the majority of the growth and yield plots, no measurements were done between 1959 and 2004.

During the late 1990's, it was decided to systematically "revive" the old field plots, most of which had been abandoned in 1959. Altogether, 65 previously abandoned plots which were recently "revived" and re-enumerated after almost 50 years without re-measurements. The distribution of these plots over the different site types and for the different forest types, characterized by the dominant species as in Table 1, is presented in Table 2.

Table 2. Summary of 65 Järvselja Research plots, presented by group of types and dominant tree species

Group of types	Pine	Spruce	Birch	Other	Total
<i>Fully drained swamp forests</i>	5		1		6
<i>Meso-eutrophic forests</i>	6	4	1		11
<i>Mesotrophic forests</i>	22	13	1		36
<i>Nemoral forests</i>		2	2	3	7
<i>Bog moss forests</i>	5				5
Total	38	19	5	3	65

The first step involved the transformation of the old handwritten entries into a digital format, which was necessary for statistical analysis and for storing the data in the multinational database, the Northern European Database of Long-Term Forest Experiments (NOLTFOX).

When analyzing and exploiting old data series like the one described above, one must be aware of possible constraints induced by uncertainties and inconsistencies in measuring and data recording. These inconsistencies can be classified according to the following categories:

- 1) *Changes in experimental design and measurement prescription.* During long period of observation, governmental policies and general research funding principles may change, which can have severe effects on financing, including termination, of ongoing long-term study projects. Old experimental designs sometimes cannot meet the demands of new research objectives, so new measurement prescriptions may be necessary. In Järvelja during the early years, the main focus was on compiling stand diameter distributions. Only a few tree heights were measured. However, soon a demand for yield tables arose, requiring tree heights for volume calculations. Subsequently, tree mapping was introduced in order to study forest spatial structures.
- 2) *High variability in measuring staff and assessment techniques.* Over long measurement periods different people are responsible for carrying out the fieldwork. The measurement accuracy within these series of consecutive enumerations may vary substantially due to changing staff. Furthermore, different measuring devices have been used over extended observation periods. In the early measurement years, tree heights were often measured using a theodolite. At the same time the heights of all the removed trees (representing the suppressed part of the plot) were measured with a measuring tape. These different methodologies could result in two different height-diameter relations.
- 3) *Changes in data recording and storing.* The biggest change in data recording was the replacement of the old handwritten experimental case files to digital data recording. During data conversion and digitizing it is possible to generate errors due to typing and misinterpretation of certain remarks in the old books. To minimize the likelihood of this type of error, special care was taken in the digitizing of the Järvelja experimental data. Outliers especially were double-checked (Hordo 2004). Nevertheless, some uncertainties still remain.

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Recognizing disturbances

In the context of this study, we distinguish between two kinds of disturbance. “Natural disturbance” refer to the number of trees which were found dead at the end of a particular measurement interval. “Anthropogenic disturbance” refers to the trees removed during a thinning operation at the beginning of a measurement interval. Figure 2 shows a typical example of a research plot which had been measured during irregular time intervals between 1926 and 1959. The shortest interval between two successive measurements was one year. The longest interval, labelled “GAP”, where data are not available during the period between 1959 and 2004, was 45 years. The measurement years in Figure 2 are indicated by black dots just below the x-axis. The graph on the left presents the quartile lines of the diameter distribution and thus shows how the forest structure has changed during the past 82 years. A pine tree which in 1895 had reached breast height (1.3 m) was cut in 2006 for stem analysis to recover the complete history of diameter and height growth. In 1920, the tree belonged to the 75% quartile of the diameter distribution. In 2006 it was in the 25% quartile of the diameter distribution.

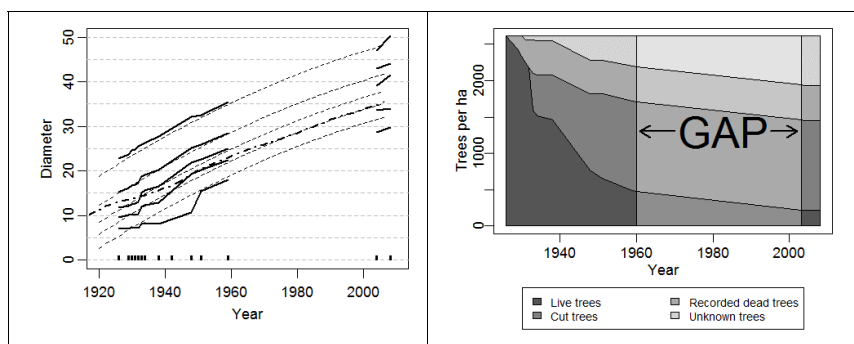


Figure 2. Empirical (solid lines) and predicted/smoothed (dashed lines) quartiles of diameter distribution over time for research plot M046_11_01 (left). The stem analysis for one pine tree is presented as a dash-dot line. The plot had been measured during irregular time intervals between 1926 and 1959, and again in 2004 and 2008 (black spots at the bottom line; the measurement years are shown in Table 3). The development of live trees and cumulative outgoing trees are shown in the graph on the right

The right-hand graph on Figure 2 shows the development of the live trees and the accumulated number of outgoing trees per ha during the 82-year observation period. At every enumeration all trees were measured, including dead snags. When trying to analyse dead trees for the entire 82-year period, during the gap period, only the number of dead trees is known, not their size distribution. Therefore, we need to distinguish between the dead trees that were recorded before 1960 and after 2004, and those that died during the gap period.

In Estonia, forest management activities are recorded in forest management plans, which provide an opportunity to recover some disturbance events. During the gap period, only sanitary cuttings were carried out in the stand, in 1974, 1976, 1977, 1980, 1996 and 1999. These cuttings removed only dead trees, but we do not know when these trees died and how many had died in a certain year. We also have no knowledge about the dimensions of the dead trees during the gap period. We know the number of trees that went missing during the gap interval and that the removed trees were not alive when cut.

For every re-measurement we calculated the accumulated number of trees cut and dead $cNx_t = \sum_{i=1}^t Nx_i$, where cNx_t refers to the accumulated number of trees separately for each cut (x =cut) and dead (x =dead) trees at the enumeration period t , Nx_i is number of trees at the enumeration period i ; t is measurement interval (years). The number of unknown trees for a particular tree species is obtained from the initial total number of trees of that species minus the cut, recorded dead and live trees. For this plot no measurements are available between 1959 and 2004. Re-measurements started again in 2004, after a “gap” of 45 years. Relevant details about the available natural and anthropogenic disturbances are listed in Table 3.

Table 3. Details about the natural and anthropogenic disturbances in research plot M046_11_01

Year	Area (ha)	Number of trees per ha			Basal area m ² per ha				Cumul. trees per ha			
		live	cut	dead	live	cut	dead	rG	NG	unknown	cut	dead
1	2	3	4	5	5	7	8	9	10	11	12	13
1926	0.06	2617			35.65			0.00	0.00			
1929	0.06	2433		183	36.97		1.54	0.04	1.75	1		183
1930	0.06	2333		100	37.54		1.21	0.03	1.32	1		283
1931	0.06	2250		33	37.22		0.22	0.01	2.46	51		316
1932	0.06	2183		67	37.33		0.50	0.01	2.25	51		383
1933	0.06	1600	500	83	32.70	4.56	0.78	0.14	1.90	51	500	466
1934	0.06	1517	67		32.48	0.99		0.03	1.43	67	567	466
1938	0.06	1467	50		35.14	0.36		0.01	3.25	67	617	466
1942	0.06		433				6.87	0.00	0.00		1050	
1948	0.06	767			30.13			0.00	0.00	1050	1050	466
1951	0.06	650	117		28.24	3.27		0.10	1.47	1167	1167	466
1959	0.06	483	67	17	25.47	2.19	0.36	0.09	1.63	1234	1234	483
2004	0.06	217			25.13			0.00	0.00	1234	1234	483
2008	0.06	217			27.92			0.00	0.00	1234	1234	483

The weight of a disturbance may be described by the ratio between removed and total basal area. We designate this variable using the symbol rG. The preference of a disturbance refers to the relative tree size removed from the population. Murray and Gadaw (1991) used the difference between the mean diameters of the removed and the remaining trees, divided by the diameter standard deviation of the whole stand to describe the type of thinning. In this study, we are using the so-called NG ratio, which is defined as follows:

$$NG = \frac{rN}{rG} = \frac{N_{thn} / N_{tot}}{G_{thn} / G_{tot}} \quad (1)$$

where N_{thn} and N_{tot} are removed and total stem number, respectively; G_{thn} , and G_{tot} are removed and total basal area, respectively. The values for rG and NG for the different measurement years are shown in columns 9 and 10 of Table 3. Evidently, the thinnings were usually weak to moderate, ranging from 1 to 14 percent of basal area removed. The NG-ratio varied between 1.32 and 3.25, indicating very low thinnings.

We also recovered disturbances for an experiment involving a mixed forest with two tree species. Figure 3 shows two graphs which correspond with pure pine plot data presented in Figure 2. The two tree species are *Betula pendula* (denoted Birch in Table 4) and *Pinus sylvestris* (denoted Pine in Table 4).

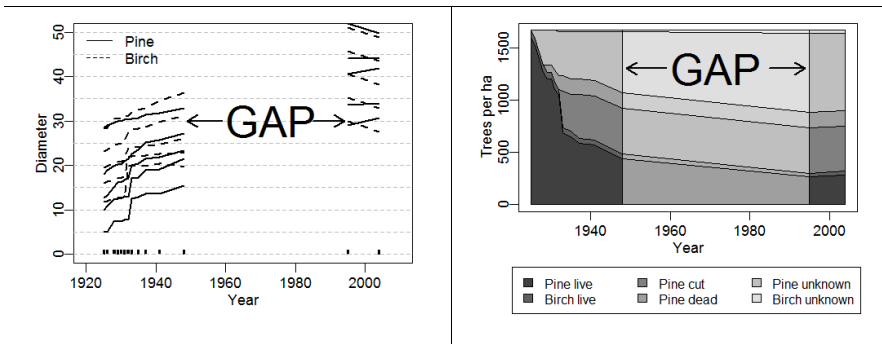


Figure 3. Development of the four quartiles of the diameter distribution of pine and birch for research plot M274_04_02 (left) and development of outgoing trees (right). The plot had been measured (spots at bottom) during irregular time intervals between 1926 and 1959, and again in 2004 and 2008

Table 4. Details about the natural and anthropogenic disturbances in research plot M274_04_02

Year	Area (ha)	Species	Number of trees (per ha)			Basal area (m ² per ha)			rG	NG	Cumul. trees per ha		
			live	cut	dead	live	cut	dead			unknown	cut	dead
1	2	3	4	5	5	7	8	9	10	11	12	13	14
1925	0.06	Pine	1600			28.47			0.000	0.000			
1926	0.06	Pine	1517			29.04			0.000	0.000	83		
1928	0.06	Pine	1267			28.47			0.000	0.000	333		
1929	0.06	Pine	1200		67	28.34		0.57	0.020	2.658	333		67
1930	0.06	Pine	1200			28.34			0.000	0.000	333		67
1931	0.06	Pine	1100		50	28.10		0.53	0.018	2.364	383		117
1932	0.06	Pine	1050		17	27.63		0.24	0.009	1.799	417		133
1933	0.06	Pine	683	350	17	22.67	5.48	0.08	0.197	1.773	417	350	150
1935	0.06	Pine	650			22.57			0.000	0.000	450	350	150
1937	0.06	Pine	583	67		22.96	1.35		0.056	1.842	450	417	150
1941	0.06	Pine	567			23.00			0.000	0.000	467	417	150
1948	0.06	Pine	433	17		20.61	1.19		0.055	0.676	583	434	150
1995	0.06	Pine	267			33.19			0.000	0.000	750	434	150
2004	0.06	Pine	283			36.47			0.000	0.000	733	434	150
1925	0.06	Birch	67			2.23			0.000	0.000			
1926	0.06	Birch	67			2.29			0.000	0.000			
1928	0.06	Birch	67			2.54			0.000	0.000			
1929	0.06	Birch	67			2.56			0.000	0.000			
1930	0.06	Birch	67			2.56			0.000	0.000			
1931	0.06	Birch	67			2.68			0.000	0.000			
1932	0.06	Birch	50			2.54			0.000	0.000	17		
1933	0.06	Birch	50			2.61			0.000	0.000	17		
1935	0.06	Birch	50			2.65			0.000	0.000	17		
1937	0.06	Birch	50			2.71			0.000	0.000	17		
1941	0.06	Birch	50			2.90			0.000	0.000	17		
1948	0.06	Birch	50			3.13			0.000	0.000	17		
1995	0.06	Birch	33			4.58			0.000	0.000	33		
2004	0.06	Birch	33			4.11			0.000	0.000	33		

The graph shows that initially the birch was dominant, which is quite common in a Pine/Birch community. After 79 years of observation, birch has lost its dominance, and both distributions are similar.

Table 4 presents relevant details of a representative plot with two species. The number of birch trees was reduced to about one half of the original number during the 79-year observation period. The number of pine trees decreased from 1600 per ha in 1925 to 283 per ha in 2004. Only 17 percent of the pines survived during the observation period.

The basal areas has been increasing due to tree growth and decreasing due to mortality and mortality-preemptive removal of some small trees that were still alive but were expected to die in the immediate future. Therefore, the values of rG and NG can be evaluated only during a particular harvest event, i.e. if we can identify the trees which were leaving the system during a specific measurement interval. The calculation schema is described by the example with one species (Table 3) and will not be repeated here.

Stand density in long-term experiments

Populations of trees growing at high densities are subject to density-dependent mortality or *self-thinning* (Mohler *et al.* 1978). For a given average tree size, there is a limit to the number of trees per hectare that may co-exist in an even-aged stand (Nilson 2006). This limiting relationship is site- and species-specific, and the topic is highly relevant to research dealing with natural disturbances. Estimating the potential density of forest stands is one of the most difficult problems to solve, mainly because data from untreated, fully-stocked stands, such as the previously abandoned plots in Järvelja, is very scarce. We analyse the potential density using two approaches, the conventional limiting relationship and Nilson's stand sparsity.

Reineke's limiting line

The relationship between the average tree size (increasing over time) and the number of live trees per unit area (declining over time) may be described by means of a so-called limiting line. A convenient model for this limiting relationship was used by Reineke (1933):

$$N_{\max} = \alpha_0 Dg^{\alpha_1} \quad (2)$$

where N_{\max} is maximum number of surviving trees per ha, Dg is quadratic mean diameter, α_0 and α_1 are empirical parameters.

The parameters of eq (2), which in its logarithmic form is linear, can be obtained from fully stocked, unthinned trials, such as the spruce growth series established in

Denmark (Skovsgaard, 1997, p. 97 et sqq.) or the *Correlated Curve Trend* (CCT) series of growth experiments established by O'Connor (1935) in South Africa (refer to Gadow 1987, for a description of the CCT experiments and examples of Reineke's limiting line fitted to the data from unthinned CCT experiments).

Nilson's stand sparsity

In the case of a regular spatial distribution of the trees within a forest, the average distance between the trees may be estimated by the square root of 10 000 (the square metres in one hectare) divided by the number of trees per ha. Nilson (1973) thus defined L , the *stand sparsity* or distance between regularly placed trees as follows

$$L = \frac{100}{\sqrt{N}} \quad (3)$$

where N is the number of trees per hectare. For a triangular placement of trees the corresponding formula would be

$$L = \frac{200}{\sqrt{3 \cdot N}} \quad (4)$$

Nilson (2006; see also Hilmi 1957) argues that the most simple and logical relation is expected between variables of the same dimension, which is not the case in eq (2), but is the case in eq (3). Therefore, Nilson (1973) proposed to estimate the potential density using the following relationship

$$L = a + b \cdot Dg \quad (5)$$

where L is the stand sparsity, and Dg is the mean squared diameter of the trees in a stand; a and b are empirical parameters.

Estimating potential density

Considering the high cost of maintaining a series of unthinned, densely-stocked stands, such data are usually not available. To overcome this deficiency, various indirect methods have to be used to estimate the limiting line. Gadow and Hui (1993) compared different methods for estimating potential density for unthinned stands of *Cunninghamia lanceolata* from the southern region of China, including the approaches used by Goulding (1972), Sterba (1975) and Clutter and Jones (1980).

We do not need such sophisticated estimation techniques because our long-term experiments had reached the limiting density. No live trees had been removed in the plots during the period 1926 to 1932 and again during the last 49 years (only the very smallest

were harvested pre-emptively, i.e. assuming that they would die anyway). Figure 4 shows the estimated limiting relation for plot *M046_11_01*, – pure pines stand in a Mesotrophic forest.

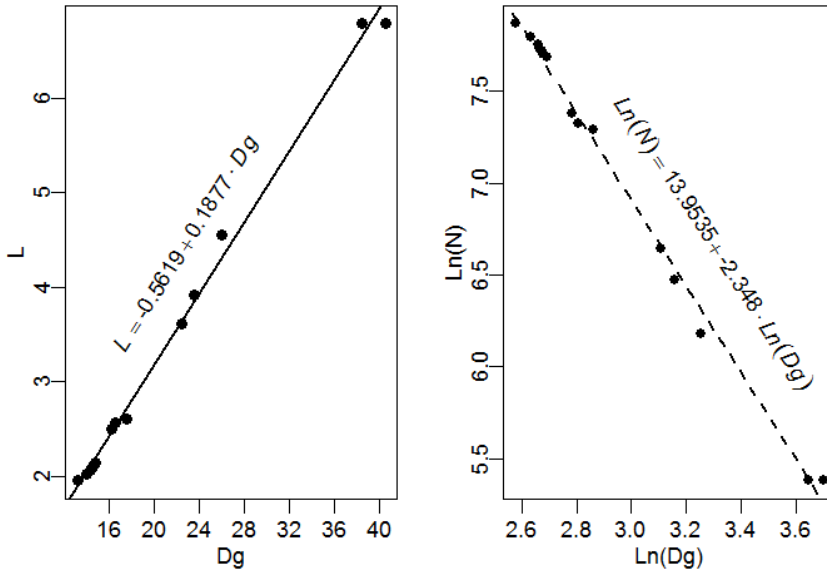


Figure 4. Nilson's Stand Sparsity estimated using eq (3, left) and Limiting Line eq (2, right) for plot *M046_11_01*

The corresponding analysis for the Pine/Birch experiment *M274_04_02* is presented in Figure 5. It is interesting to note the differences in the slopes and intercepts of the limiting relationships for pine and birch, given the specific relative proportions of tree numbers during the entire measurement period. In 1925, there were 67 birch and 1600 pine trees per ha. Thus four percent of the trees were birch and 96 percent pine. In 2004, ten percent of the trees were birch.

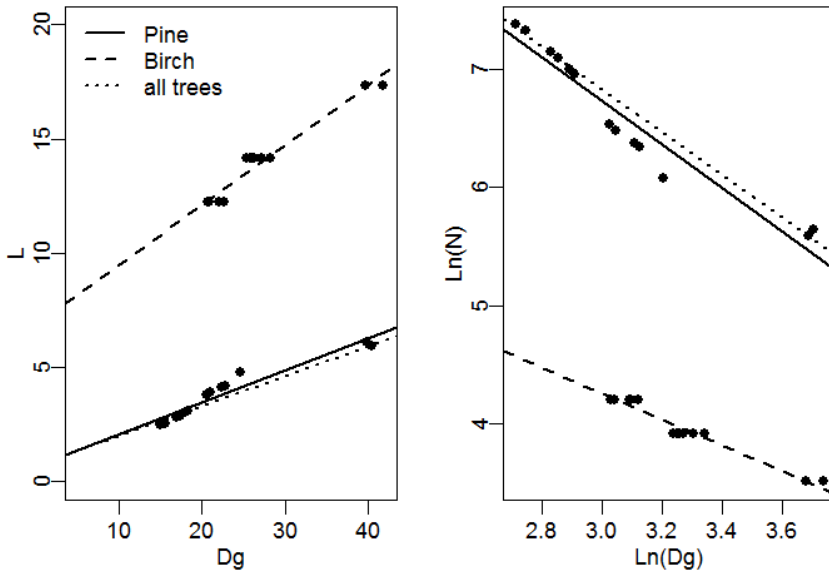


Figure 5. Nilson's Stand Sparsity estimated using eq (3, left) and Limiting Line eq (2, right) separately fitted for birch and pine trees in plot M274_04_02.

Birch and pine are both light-demanding species and their shade tolerance decreases rapidly growing out of the seedling stage. At the beginning of the plot enumeration, the diameter distributions in Figure 3 show that the birch trees were dominant. This effect can also be seen in the early Dg-values of pine and birch in the left graph of Figure 5. Later on, after reaching a Dg of more than 40 cm, the mean diameters of pine and birch trees are almost equal. This result is not (only) due to growth, but mainly due to higher mortality of the pines in the lower ranges of the diameter distribution.

The slope parameter values of the stand sparsity line are indicative of the mortality rates for a given increase in Dg. The values in Figure 5 are 0.14 for pine and 0.26 for birch, and 0.13 for the whole population. The slope for pine slightly exceeds the slope for the whole stand. This implies a higher pine mortality rate per unit of Dg increase. The beauty of Nilson's stand sparsity, in contrast to the widely used Reineke line, is that it allows such clear, easily understood interpretations.

Discussion and conclusions

Pickett *et al.* (1987) distinguish between pathways, causes and mechanisms of vegetation change in order to explain the dynamics of succession. They define a pathway as a temporal pattern of vegetation change and a cause as an agent, circumstance or action responsible for successional patterns. Permanent field plots can provide observations about pathways of succession, but may also generate hypotheses on mechanisms and causes. This is especially relevant if the communities are protected from human interference, but is also valid in managed forests where the objective is to explain particular response patterns following specific harvesting operations.

In this study, we defined the problem of analyzing disturbances for irregular measurement interval within the general context of forest research in Estonia. We presented examples of previously abandoned experiments which have recently been re-measured, and proposed a method which can be used to estimate historical disturbances on a specific field plot and during a particular measurement gap.

Considering the enormous investment and its usefulness for environmental research, the national importance and scientific relevance of the Estonian Forest Research database is evident. Valuable observations have been diligently collected by several generations of scientists, providing information about forest structure (Mathiesen and Riisberg 1932, Tullus and Reisner 1998, Kangur *et al.* 2007), disturbances and ecosystem dynamics in the different forest types (Kiviste *et al.* 2005). The maintenance of such a key database is considered to be of national importance in most countries today (Sims *et al.* 2006).

The history of empirical forest research in Estonia began with the establishment of well-designed and documented field experiments in the Järvselja Forestry Training and Research Centre in 1921. Among the early long-term forest experimental series in Järvselja are growth and yield experiments established by Andres Mathiesen between 1922 and 1935 (Kasesalu 2003). The measurement data were stored in handwritten data journals and experiment case files. The last of these handwritten records dates back to 1959. During the late 1990's it was decided to systematically "revive" the old field plots most of which had been abandoned in 1959. This study has shown ways to analyze human and natural disturbances for specific measurement intervals using variables which allow interpretation of the weight of the disturbance as well as its type.

We have also been able to show potential densities for a pure pine plot and a mixed pine/birch experiment using the common Reineke line and Nilson's stand sparsity. The slope parameter values of the stand sparsity line are indicative of the mortality rates for a given increase in D_g . This study has shown a higher pine mortality rate per unit of D_g increase in the mixed plot. The advantage of Nilson's stand sparsity, in contrast to the widely used Reineke line, is the fact that both variables have the same unit, which facilitates interpretations.

The natural decline of the number of surviving trees in an unthinned forest is usually characterized by intermittent brief spells of high mortality, followed by long periods of low mortality. The process is not a continuous one (Boardman 1984, Gadow 1987, p. 21). Stochastic models have been used in some cases to mimic these processes. However, for the purpose of simulating alternative silvicultural regimes, it is generally assumed that natural mortality is a continuous process. Based on the analysis in this paper, we are convinced that Nilson's approach is very useful in estimating the maximum density in Estonian forests, for different stand and site types. This topic will be pursued in future studies based on the extensive database of the Estonian Forest Research Plots Network.

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ИССЛЕДОВАНИЕ ИЗМЕНЕНИЙ В ХОДЕ РОСТА ДРЕВОСТОЕВ ОБУСЛОВЛЕННЫХ НАРУШЕНИЯМИ ЛЕСА НА БАЗЕ НЕРЕГУЛЯРНЫХ ИЗМЕНЕНИЙ ПОСТОЯННЫХ ПРОБНЫХ ПЛОЩАДЕЙ В УЧЕБНО-ОПЫТНОМ ЛЕСНИЧЕСТВЕ ЯРВСЕЛЯ

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Резюме

На основе повторных измерений постоянных пробных площадей можно получить информацию о сукцессии леса, а также постановить гипотезы об её механизме и причинах. Это уместно не только к лесным сообществам, защищенным от человеческого вмешательства, то также и к хозяйственным лесам, где целью исследования является изучение результатов специфических операций пользования лесом.

Учреждение и проведение долговременных наблюдений постоянных пробных площадей требует твердого посвящения исследователей в условиях краткосрочных экономических колебаний и политических изменений. Однако, эксперименты, первоначально разработанные для длительных промежутков времени, могут быть преждевременно оставлены из-за нехватки финансирования или изменения политики. Одним из аспектов, получившим мало внимания в прошлом, является "возрождение" ранее заброшенных постоянных пробных площадей. В этой работе анализируются данные долгосрочных лесных экспериментов в учебно-опытном лесничестве Ярвселя заброшенных в 1950-ых годах и „возрожденных“ в 1995 и 2004 годах.

Данное исследование различает два вида лесной нарушений: естественное и антропогенное. „Естественное нарушение“ леса основывается на количестве деревьев, которые были мертвыми к концу определенного интервала времени. „Антропогенное нарушение“ леса основывается количестве деревьев, которые были вырублены в течение данного интервала времени. Величины обоих видов нарушений леса оценивались исходя из количества биомассы и относительных размеров опадающих деревьев. Наконец, в данной работе смертность при предельной густоте (зависимость самоизреживания) анализируется по закономерностям, уставленным Рейнке и Нильсоном. По данным этой работы, подход Нильсона является более предпочтительным для интерпретации зависимости самоизреживания в смешанных лесах и для оценивания максимальной густоты для разных древостоев и условий местопроизрастания.

Ключевые слова: долговременные лесные опыты, разрыв между измерений, линия самоизреживания по Рейнике, редкость древостоя по Нильсону



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Comparative modeling of stand development in Scots pine dominated forests in Estonia

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Abstract

In general, forests in Estonia are characterized by great variability, not only in protected areas but in commercial forests as well. The data needed for the derivation and calibration of growth models can be obtained by continuous observation of permanent growth plots (also known as longitudinal studies) or by establishing chronosequences with temporary plots distributed over a wide range of growing sites, densities and ages (also known as cross-sectional studies). A compromise may be achieved by a system of “interval plots” (also known as a short-time series: series which covers a short time). Since the measurement interval is a period of undisturbed growth, it is possible to measure change rates as in a longitudinal study and at the same time cover a wide range of initial conditions as in a cross-sectional study. Numerous models of stand growth have been derived from re-measured sample plots. This study, which uses the data of 142 five-year intervals from 134 unmanaged Scots pine stands, compares six different model combinations involving algebraic difference equations and fixed time-step increment equations. New stand-level diameter and basal area increment equations and a tree survival model which showed close correspondence with the existing stand-level model for Estonia were developed. The main advantage of the use of algebraic difference equations over the fixed-step increment equations is the ability to use flexible time steps. However, the projection intervals should not deviate too much from the time steps of the measurement data. An important constraint when using the algebraic difference equations is to avoid long-term predictions in one projection sequence.

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Keywords: Forest management planning; Short-term growth modeling; Interval plots; Algebraic difference equation; Fixed-step increment equation

1. Introduction

In many regions of the world, people depend on forests for their livelihood and well-being. Forests represent an important renewable reservoir of raw materials for the wood processing industry and a remnant wilderness of high recreational and spiritual value in urbanized societies. To meet the demands of society, foresters have been developing silvicultural treatment schedules which are assumed to be optimal for a given set of site and market conditions. Changes in human populations, cultures and attitudes can rapidly shift the effect of human intervention on the natural processes. These shifts alter the patterns of anthropogenic disturbance and lead to changes in patterns of natural disturbance which became apparent many decades later (Oliver and Larson, 1996).

Forest dynamics is affected by many processes at different levels of ecosystem regulation. The growth and change in the number of trees belonging to various age and size classes has been a classic approach to describing forest dynamics. However, the long-term processes include great variation in the factors affecting the dynamic patterns of forest development. The patterns of change shows considerable variation on the temporal and spatial scale: a great number of trees can be removed from a stand within a short period (natural disturbances, cuttings) or the number of trees may decrease gradually by natural mortality or gap formation (Kangur et al., 2005).

There has been considerable debate about empirical modeling of stand growth and yield processes. The purpose of using a growth model is to make reasonable predictions about tree growth and stand development, which may be achieved in different ways and at varying levels of detail, depending on the data available about the trees and the growing site. Models based on stand variables have been used for more

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Nomenclature

c_1, \dots, c_4	regression coefficients
D_t, D_{t_1}, D_{t_2}	stand quadratic mean diameter (cm) at the age of t, t_1 and t_2 , respectively
D_{t+5}	stand quadratic mean diameter for the next 5-year period (cm)
ΔD_{t+5}	5-year stand quadratic mean diameter increment (cm per 5-year period)
G_t, G_{t_1}, G_{t_2}	stand basal area (m^2/ha) at age t, t_1 , and t_2 , respectively
G_{t+5}	stand basal area (m^2/ha) at the end of the 5-year period
ΔG_{t+5}	stand basal area increment in 5-year periods (m^2/ha per 5 years)
H_t, H_{t_1}, H_{t_2}	stand mean height (m) at the age of t, t_1 and t_2 , respectively
H_{100}	site index (stand mean height (m) at the age of 100 years)
HF	form height (m)
L_t	stand sparsity (average distance between trees (m)) at age t
L_{t+5}	stand sparsity at the end of the 5-year period (m)
ΔL_{t+5}	5-year stand sparsity change (m)
N_t, N_{t_1}, N_{t_2}	stand density (the number of trees per hectare) at age t, t_1 , and t_2 , respectively
N_{t+5}	stand density (the number of trees per hectare) at the end of the 5-year prediction
OHOR	thickness of soil organic layer (cm)
P_{t+5}	tree survival probability after the 5-year period
R	correlation coefficient
RMSE	root mean square error
RD_t	degree of stocking at age t
V_t, V_{t_1}, V_{t_2}	stand volume (m^3) at the age t, t_1 and t_2 , respectively
Δy	observed change
$\Delta \hat{y}$	predicted change
Greek letter	
ε	error component

practical purposes. Single-tree modeling leads to greater flexibility in attempting to use details of spacing (Hägglund, 1981; Söderberg, 1986; Nabuurs and Päivinen, 1996; Hynynen et al., 2002; Pretzsch et al., 2002; Hasenauer, 2005).

Since most growth and yield models are developed on the basis of existing empirical data, the most appropriate modeling technique is determined by the level of detail of the available data and the level of resolution of the projection. The data needed for development and calibration of growth models can be obtained by continuous observation of permanent growth plots (also known as longitudinal studies) or by establishing chronosequences with temporary plots distributed over a wide

range of growing sites, densities and ages (also known as cross-sectional studies). A compromise may be achieved by a system of “interval plots” (also known as a short-time series: series which covers a short-time). Since the measurement interval is a period of undisturbed growth, it is possible to measure change rates as in a longitudinal study and at the same time cover a wide range of initial conditions as in a cross-sectional study (Glenn-Lewin and van der Maarel, 1992; Gadov and Hui, 1999).

Forest growth and yield tables have traditionally been used in Estonia to offer predictions of forest growth for decision-making in forest management planning. In general, the forests in Estonia are characterized by wide variability in tree species composition and stand structure, both in protected areas and commercial forest (Pärt et al., 2006). The great natural diversity of our forests in combination with the growing role of environmental and socio-cultural values in forest management planning has created a situation in which traditional growth and yield tables do not meet these new requirements (Nilson, 1996, 1999).

A considerable number of growth and yield tables (Krigul, 1969; Kiviste, 1988), several stand growth equation systems (Tappo, 1982; Kiviste, 1999a,b) and some single-tree models (Jõgiste, 1998) have already been developed for stand growth prediction in Estonia. Most of those models are available for public use and have been incorporated into the Database of Forest Management Models (ForMod) which provides open access through an internet-based information system (Sims, 2003, 2005). In principle, the existing growth and yield tables and growth equation systems in Estonia have been created for long-term general growth and yield prediction for practical forest management planning at landscape level.

The concept of adaptive forest management planning has been elaborated in Estonia by Nilson (1996). The idea of this method is adaptive planning of the cutting age for every stand depending on its individual characteristics. The full exploitation of this method requires more detailed growth model systems for stand-level modeling than we have today. An Estonian network of permanent forest growth plots for modeling stand variables and construction of stand growth simulators, which require individual tree growth measurement series, was established in 1995 (Kiviste and Hordo, 2003).

For predicting the main stand variables (height, diameter, density, basal area and volume) requires a complete set of models including both growth and static models. One of the objectives of the current study was the development of short-term stand growth models based on interval plot data for analyzing the performance of various sets of growth models to predict Scots pine dominated stand development during a period of undisturbed growth. The individual model components may be combined in many ways to predict the growth of previously disturbed stands as a whole using the changed initial state of stands functioning as growth predictors as the indirect indicators of previous disturbances. We might thus expect to see great differences when using different types of model with different combinations of predictor variables. Accordingly, the second objective of this study was to analyze various simulation

combinations to find the best set of model components for describing short-term Scotch pine stand growth.

2. Material and methods

This section introduces the Estonian network of permanent forest growth and yield plots. We also describe the type of growth model used.

2.1. Interval measurement data

For the study of growth and yield of Estonian forests, we used 5-year interval measurement data provided by the Estonian network of permanent forest growth and yield monitoring plots. This network was established in 1995 and was designed using experience of Finnish studies (Gustavsen et al., 1988) to provide empirical data for developing forest growth and yield models (Kiviste and Hordo, 2003). The 679 permanent growth and yield monitoring plots were distributed randomly in 2–10 plots clusters over the entire land surface of Estonia, mainly following the grid of ICP Forest level I monitoring plots (Karoles et al., 2000). The spatial distribution of the plot cluster locations appears in Fig. 1.

The network of permanent plots covers the main forest types and the age range of typical commercial forests in Estonia, re-measurements on the permanent plots being carried out at 5-year intervals. The plots are of circular shape with varying radius, containing at least 100 upper storey trees. The polar coordinates and breast height diameters of all trees are assessed on each plot. In addition, the total tree height and crown length of selected sample trees are measured (Kiviste and Hordo, 2003). The dataset from the re-measurements of 679 plots includes almost 190,000 single-tree measurements.

For this study, Scots pine dominated plots were selected from the database. The stand was considered as pine dominated

if the proportion of pine volume exceeded 50%. Since most of the plots selected were pure pine stands (93% of trees on selected plots being pines) all other tree species in the main storey included in model development and for stand mean variables (H , D , N , G , V) calculation were considered as Scots pine. The 5-year changes in stand height (H), quadratic mean diameter (D), density (N), basal area (G) and volume (V), at various measurement intervals appear in Fig. 2.

The current study used 142 growth intervals from 134 unmanaged Scots pine dominated plots (Table 1), the average size being 0.1456 ha. Since no silvicultural treatments took place in these plots during the monitoring period, the data represents the stand growth over a 5-year growth interval, undisturbed by forest management. Unfortunately, since there are no reliable records available about the previous management in these plots, we applied a modeling technique "without memory" in which the prediction is a function of the initial system state.

2.2. Model components

Several model components are presented in this section, including difference models based on Estonian forest inventory data and an alternative set of growth models based on interval plot data.

2.2.1. Difference models based on Estonian forest inventory data

The algebraic difference models of Kiviste (1999a,b) are being employed as general growth and yield prediction functions in practical forest management planning in Estonia. These models were developed from Cieszewski and Bella type stand growth equations (1989). The model parameters were estimated using the data of the state forest inventory in Estonia in 1984–1993 (Kiviste, 1995, 1997). The average height, quadratic mean diameter at breast height, and volume of

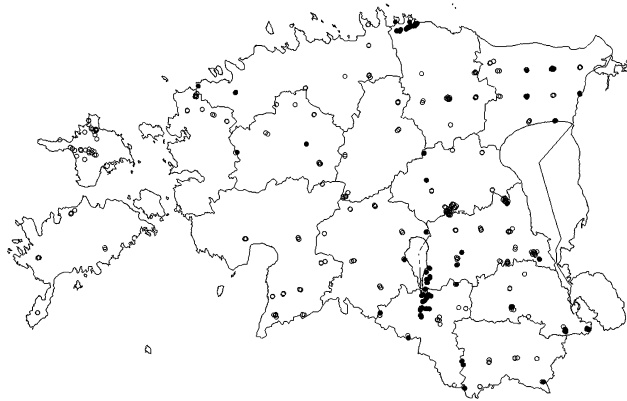


Fig. 1. Geographic location and spatial distribution of Estonian network of permanent forest growth and yield monitoring plots. Each circle on the map presents a cluster of 2–10 sample plots. On the map the circles represent all monitoring areas and the filled dots Scots pine dominated sample plots used in this study.

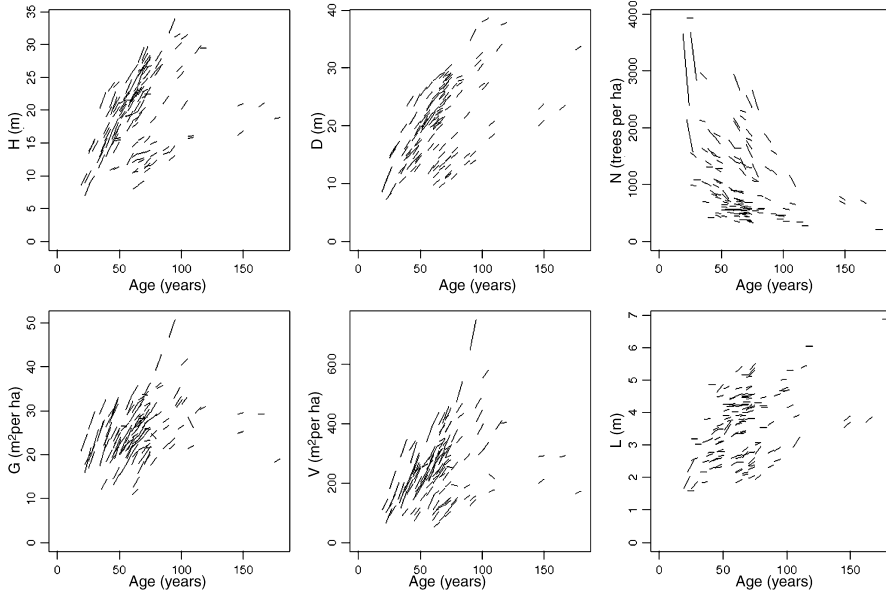


Fig. 2. Change in height (*H*), diameter (*D*), density (*N*), basal area (*G*) and volume (*V*) over age and LD relationship in Scots pine dominated stands on the Estonian network of permanent forest growth and yield monitoring plots.

423,919 stands were grouped by forest site type, dominant tree species, stand origin (naturally regenerated or cultivated), and stand age-class (using 5-year intervals). This grouping produced a total of 171 age-series of height, diameter, and volume. Data from young stands (under 20 years for coniferous and hardwood, and 10 years for deciduous forests), over-mature stands and outliers were excluded before the calculation.

Kiviste’s difference models were developed from stands in which both natural and anthropogenic disturbances were included. The presumed maximum stand age in these models was fitted with the optimal rotation period of the dominant tree species. In pine-dominated stands this age is 120 years. Future stand mean height (H_{t_2}) at the desired age (t_2) was calculated from the initial age (t_1) and height (H_{t_1}) as follows:

$$H_{t_2} = \frac{H_{t_1} + dH + rH}{2 + 4\beta H(t_2^{-1.58})/H_{t_1} - dH + rH} \tag{1}$$

where $\beta H = 8319 - 493 \ln(\text{OHOR} + 1)$, $dH = \beta H/50^{1.58}$ and $rH = \sqrt{(H_{t_1} - dH)^2 + 4\beta H H_{t_1}/t_1^{1.58}}$.

The stand quadratic mean diameter (D_{t_2}) at the desired age (t_2) was calculated as follows:

$$D_{t_2} = \frac{D_{t_1} + dD + rD}{2 + 4\beta H(t_2^{-1.33})/D_{t_1} - dD + rD} \tag{2}$$

where $\beta D = 6051 - 306 \ln(\text{OHOR} + 1)$, $dD = \beta D/50^{1.33}$, $rD = \sqrt{(D_{t_1} - dD)^2 + 4\beta D D_{t_1}/t_1^{1.33}}$.

The stand volume (V_{t_2}) at the desired age (t_2) was calculated as follows:

$$V_{t_2} = \frac{V_{t_1} + dV + rV}{2 + 4\beta H(t_2^{-1.93})/V_{t_1} - dV + rV} \tag{3}$$

Table 1
Summary statistics of 142 growth intervals of unmanaged Scots pine dominated monitoring plots

Variable	Minimum	0.25 quantile	Mean	0.75 quantile	Maximum
Stand age (years)	19.0	50.0	63.5	70.0	175.0
Basal area (m ² /ha)	10.8	20.8	24.5	28.4	46.7
Quadratic mean diameter (cm)	7.2	14.4	19.9	24.7	38.0
Stand density (stems/ha)	212.2	551.3	1039.0	1387.0	3930.0
Stand height (m)	6.9	13.9	19.0	22.9	31.7
Stand volume (m ³ /ha)	53.0	157.3	231.0	284.8	647.0

where $\beta V = 380,540 - 54,348 \ln(\text{OHOR} + 1)$, $dV = \beta V / 50^{1.93}$ and $rV = \sqrt{(V_{t_1} - dV)^2 + 4\beta V V_{t_1} / t_1^{1.93}}$.

2.2.2. Growth models based on interval plot data

The predictor variables (quadratic mean diameter, stand density, basal area and sparsity) should be selected as closely as possible to the originally measured variables for reducing the error propagation, collinearity and variance inflation generated during derivation. The model forms should be selected according to the principles of model simplicity (i.e., parameter parsimony) (Burkhardt, 2003) and biological realism (Gadow, 1996; Schmidt et al., 2006). The following equations were selected to describe the change in stand variables (growth and survival). The following model was used for stand basal area growth:

$$\Delta G_{t+5} = c_1 e^{-c_2 D_t} + c_3 H_{100} + c_4 G_t + \varepsilon \tag{4}$$

where ΔG_{t+5} is the stand basal area increment in a 5-year period (m^2/ha per 5 years), D_t the stand quadratic mean diameter (cm) at the beginning of the 5-year period, H_{100} the site index (stand mean height (m) at the age of 100 years), G_t the stand basal area (m^2/ha) at the beginning of the 5-year period, c_1, \dots, c_4 the regression coefficients and ε is the error component. Stand basal area at the end of the 5-year period (G_{t+5}) can be calculated as follows:

$$G_{t+5} = G_t + \Delta G_{t+5} \tag{5}$$

The following regression equation was applied to estimate the stand quadratic mean diameter increment ΔD_{t+5} :

$$\Delta D_{t+5} = c_1 + c_2 D_t + c_3 H_{100} + c_4 G_t + \varepsilon \tag{6}$$

Stand quadratic mean diameter at the end of the 5-year period (D_{t+5}) can be calculated as follows:

$$D_{t+5} = D_t + \Delta D_{t+5} \tag{7}$$

A classic approach to predicting stand density at the end of a 5-year period is to estimate the probability of tree survival (P_{t+5}) during the prediction interval (Vanclay, 1994). The logistic equation with logit-transformation was used for this purpose:

$$P_{t+5} = \frac{e^x}{1 + e^x} \tag{8}$$

with $x = c_1 + c_2 \text{RD}_t + c_3 D_t + c_4 H_{100} + \varepsilon$, where RD_t is degree of stocking at age t . The number of trees per hectare at the end of the period (N_{t+5}) is calculated as follows:

$$N_{t+5} = N_t P_{t+5} \tag{9}$$

Hart (1928) proposed calculating the average distance between the trees in a forest with N stems per hectare as the square root of the growing space $L = \sqrt{10,000/N}$. This approach assumes regular spacing of trees. The variable L is known as the sparsity of a stand (average distance between trees (m) at time t). The linear dependence between stand mean diameter and stand sparsity has been shown by earlier studies (Nilson, 1973, 2005). Following Nilson, we fitted the separate

tree distance based regression equation for estimating the development of variable L :

$$\Delta L_{t+5} = c_1 + c_2 D_t + c_3 H_{100} + G_t + \varepsilon \tag{10}$$

where ΔL_{t+5} is the 5-year stand sparsity change. Stand sparsity at the end of the 5-year period (L_{t+5}) can be calculated as follows:

$$L_{t+5} = L_t + \Delta L_{t+5} \tag{11}$$

The difference equation for tree survival published by Gurjanov et al. (2000) was used:

$$N_{t_2} = 1000 \times \left[\left(\frac{N_{t_1}}{1000} \right)^{c_1} + c_2 (H_{t_2}^{c_3} - H_{t_1}^{c_3}) \right]^{1/c_1} + \varepsilon \tag{12}$$

where N_{t_1} is the number of trees per hectare at the beginning of the prediction period and N_{t_2} is the number of trees per hectare at the end of the prediction period.

For describing basal area growth, the difference equation presented by Gadow and Hui (1999) was applied:

$$G_{t_2} = G_{t_1} N_{t_2}^{1-c_1 H_{t_2}^2} N_{t_1}^{c_1 H_{t_1}^2 - 1} \left(\frac{H_{t_2}}{H_{t_1}} \right)^{c_3} + \varepsilon \tag{13}$$

where G_{t_2} is stand basal area (m^2/ha) at the end of the prediction period.

For comparison of model fit, we calculated the predicted change ($\Delta \hat{y} = \hat{y}_2 - y_1$) and observed change ($\Delta y = y_2 - y_1$) during the period for every model. The correlation coefficient (R) and root mean square error (RMSE) between predicted $\Delta \hat{y}$ and observed Δy were calculated to analyze the model residuals.

2.3. Designing simulation combinations

Six different simulation combinations were used to analyze model predictions of five important stand variables (height, quadratic mean diameter, density, basal area and volume) at the end of a 5-year prediction period. Table 2 shows the calculations of projected stand variables in these combinations. In simulation combinations, some stand variables were calculated using growth models (Eqs. (1)–(13)) while other variables were calculated using static models (Eqs. (14)–(16)). The calculations of stand variables differ in simulation combinations in the use of different formulas or different calculation sequences. The simulations were carried out on the data on 142 intervals from the Estonian network of permanent growth and yield sample plots. Stand volume, form height and degree of stocking in the simulations were calculated according to the Estonian forestry inventory practice:

$$V_t = \text{HF}_t G_t \tag{14}$$

$$\text{HF}_t = H_t \times \left(-0.0309 + \frac{2.5936}{H_t} + -0.0617\sqrt{H_t} + 0.2107 \ln(H_t) \right) \tag{15}$$

Table 2

The sequence of modeling steps and equations used in simulation combinations showing the sequence of calculation of projected variables with corresponding formula or formula reference of each simulation

Simulation combination	Sequence of model components in the six simulation combinations				
	1	2	3	4	5
$D \times G$	$H_{t_2} = \text{Eq. (1)}$	$D_{t_2} = \text{Eq. (7)}$	$G_{t_2} = \text{Eq. (5)}$	$N_{t_2} = \frac{40,000 G_{t_2}}{\pi D_{t_2}^2}$	$V_{t_2} = \text{Eq. (14)}$
$D \times L$	$H_{t_2} = \text{Eq. (1)}$	$D_{t_2} = \text{Eq. (7)}$	$N_{t_2} = \left(\frac{100}{\text{Eq. (11)}}\right)^2$	$G_{t_2} = \frac{\pi N_{t_2} D_{t_2}^2}{40,000}$	$V_{t_2} = \text{Eq. (14)}$
$D \times N$	$H_{t_2} = \text{Eq. (1)}$	$D_{t_2} = \text{Eq. (7)}$	$N_{t_2} = \text{Eq. (9)}$	$G_{t_2} = \frac{\pi N_{t_2} D_{t_2}^2}{40,000}$	$V_{t_2} = \text{Eq. (14)}$
$G \times N$	$H_{t_2} = \text{Eq. (1)}$	$G_{t_2} = \text{Eq. (5)}$	$N_{t_2} = \text{Eq. (9)}$	$D_{t_2} = \sqrt{\frac{40,000 G_{t_2}}{\pi N_{t_2}}}$	$V_{t_2} = \text{Eq. (14)}$
Dif	$H_{t_2} = \text{Eq. (1)}$	$N_{t_2} = \text{Eq. (12)}$	$G_{t_2} = \text{Eq. (13)}$	$D_{t_2} = \sqrt{\frac{40,000 G_{t_2}}{\pi N_{t_2}}}$	$V_{t_2} = \text{Eq. (14)}$
Est	$H_{t_2} = \text{Eq. (1)}$	$V_{t_2} = \text{Eq. (3)}$	$D_{t_2} = \text{Eq. (2)}$	$G_{t_2} = \frac{V_{t_2}}{\text{Eq. (15)}}$	$N_{t_2} = \frac{40,000 G_{t_2}}{\pi D_{t_2}^2}$

$$RD_t = \frac{V_t}{-30.5946 + 16.6305H_t + 0.0254H_t^2} \tag{16}$$

The root mean square errors (RMSE) were calculated for each stand variables in all simulation combinations.

3. Results and discussion

The growth and yield models routinely used in decision support systems for forest management planning in general lack sensitivity to the interactions of successional dynamics over various ages. They are stand development curves fitted to observed stand growth data describing the net production of a stand of trees. The trend in forest management planning towards ecosystem-based forest management principles has created a need to apply more sophisticated decision support systems. Several more detailed modeling approaches, such as individual tree models using competition indices, hybrid and process based models have already been developed and applied. One way of strengthening the traditional growth and yield modeling approach is to construct compatible tree and distribution models in addition to stand-level models (Richardson et al., 2006).

3.1. Model parameter estimates

Table 3 shows the parameter estimates for the growth models both developed and calibrated from the data on 142 intervals of unmanaged interval plots dominated by Scots pine. The fit statistics *R* and RMSE of these models are not comparable in the case of different dependent variables, but different equations for the same dependent variable are comparable (e.g., Eq. (4) with Eq. (13) for basal area prediction and Eq. (8) with Eq. (12) for survival prediction). The fit statistics (*R* = 0.655 and RMSE = 0.952) of the basal area growth model (Eq. (4)) for 5-year growth projection show better results than those for the basal area difference model (Eq. (13)). Similarly, the fit statistics (*R* = 0.530 and RMSE = 0.045) of the survival probability model (Eq. (8)) perform better than those of the survival difference model (Eq. (12)).

An important aspect of increment functions is that because the actual increment rates are estimated directly from the observed data, the functions are based on a limited set of independent variables (Hasenauer, 2005), but this also restricts prediction of stand variables for a given time interval (usually 5 years, depending on the calibration data measuring interval). The prediction of stand development using algebraic difference

Table 3
Parameter estimates and fit statistics for growth models based on unmanaged Scots pine interval plot data

Model	Parameter estimates				<i>R</i>	RMSE
	c_1	c_2	c_3	c_4		
Basal area growth model (Eq. (4))	12.0422	0.1712	0.1039	-0.0506	0.655	0.952
Diameter growth model (Eq. (6))	1.1909	-0.0256	0.0403	-0.0198	0.585	0.336
Survival probability model (Eq. (8))	3.7012	-0.0210	-2.5612	0.0997	0.530	0.045
Stand sparsity model (Eq. (10))	0.1103	-0.0033	-0.0004	0.0017	0.246	0.075
Gurjanov et al. survival diff. model (Eq. (12))	-2.1023	0.0002	2.5313		0.363	0.055
Gadow and Hui basal area diff. model (Eq. (13))	0.8747	-0.0340	0.9732		0.640	1.134

R: correlation coefficient between observed Δy and predicted $\Delta \hat{y}$; RMSE: root mean square error.

Table 4
RMSE values of projected vs. observed stand variables at the end of the 5-year prediction period according to different simulation combinations

Simulation combination	<i>H</i>	<i>D</i>	<i>N</i>	<i>G</i>	<i>V</i>
<i>D</i> × <i>G</i>	0.617	0.336	98.232	0.952	21.252
<i>D</i> × <i>L</i>	0.617	0.336	105.634	0.935	21.107
<i>D</i> × <i>N</i>	0.617	0.336	99.434	0.986	21.138
<i>G</i> × <i>N</i>	0.617	0.340	99.434	0.952	21.252
Dif	0.617	0.584	94.850	1.132	24.585
Est	0.617	0.395	160.204	1.695	24.194

models offers more flexibility in terms of prediction interval length.

3.2. Comparing different combinations of model components

The RMSE has been calculated for every stand variable in the simulations (Table 4). In all simulation combinations, the stand height was the first projected variable in the calculation sequence obtained by the same stand height model (Eq. (1)) and where the same RMSE value (0.617 m) occurred. The set of RMSE values showed negligible difference for the first four simulation combinations in Table 4, where projected variables were calculated based on increment equations.

The “Dif” simulation combination showed considerably higher RMSE values for quadratic mean diameter, basal area and volume calculations. It has a higher RMSE, because the

stand density and height were predicted independently, and especially since the height model was calculated using a different data set. Both height and stem number already contain a prediction error. The results of the “Est” combination showed the highest RMSE values in stand basal area and density calculations. Both variables were calculated via volume and form height (HF, Eq. (14)) and were therefore dependent on the prediction error of the form height model. Fig. 3 shows poorer performance between the observed and predicted basal area of the “Dif” and “Est” simulation combinations in comparison with other simulation combinations. The solid line in Fig. 3 generated by Kernel regression indicates the bias between the observed and predicted basal areas.

The simulation combinations in which diameter was predicted directly using growth equation (7) showed the lowest RMSE values for quadratic mean diameter. The simulations with different combinations of diameter, basal area and tree survival models conducted in the current study showed that the “*D* × *G*”, “*D* × *N*”, “*D* × *L*” and “*G* × *N*” combinations give almost as good or better results than the difference equations.

3.3. Long-term simulation of stand development

We can only predict growth and survival if the interval is a period of undisturbed growth. However, to evaluate different management scenarios, we must be able to model the disturbance events as well as the growth. A basic assumption with interval plots is that the interval is a period of undisturbed

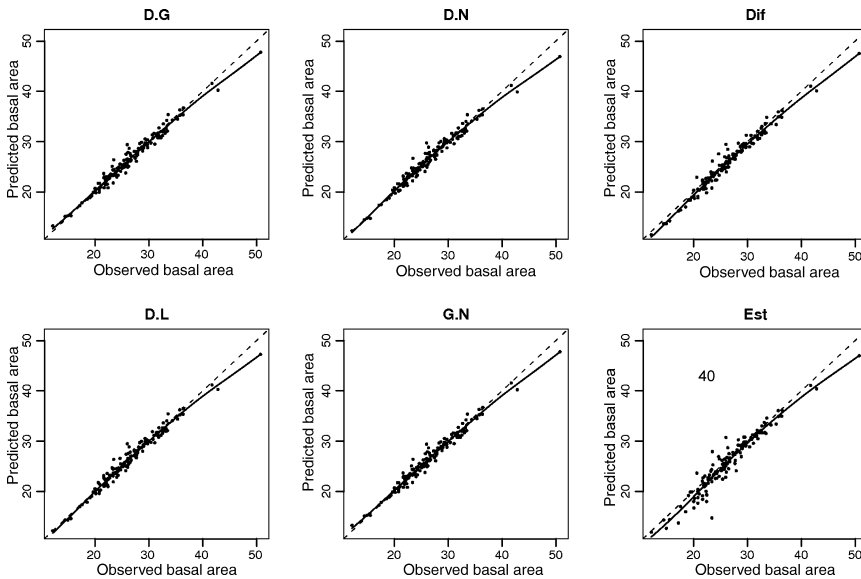


Fig. 3. Observed vs. predicted basal area for various simulation combinations. Note the systematic underestimation in stands with very large basal areas.

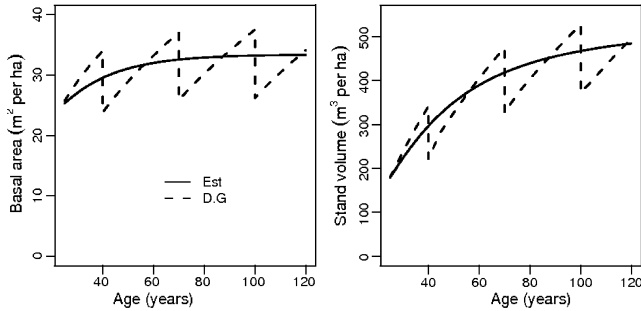


Fig. 4. An example of long-term prediction with the “Est” and “ $D \times G$ ” simulations. The initial data from one sample plot was used ($A = 25$ years, $D = 14.4$ cm, $H = 13.3$ m, $G = 25.7$ m³/ha, $V = 179$ m³/ha).

growth. All models in this study, except the Kiviste difference equations (Kiviste, 1999a,b), were developed or calibrated on the undisturbed interval plot data. The growth models include natural growth and natural single-tree survival but they do not include anthropogenic interference as can be expected in the case of commercial forests. These models therefore allow us to predict stand growth in commercial forests between harvest events in the long run.

“Est” simulation models have been developed on the basis of forest inventory data, which contain both natural mortality (gap phase disturbances) and thinnings and can be used for long-term prediction. The use of growth models developed on interval plot data in long-term prediction necessitates including both natural and anthropogenic disturbances. An example of the long-term prediction of stand basal area and volume development simulated with the “ $D \times G$ ” simulation combination in comparison with “Est”, which represents the average development of Estonian stands, appears in Fig. 4. In the

“ $D \times G$ ” model combination (Table 2), calculations were repeated with 5-year intervals up to 120 years, and the degree of stocking was calculated for every step with the Eq. (16) model. When the degree of stocking exceeded a value of 0.9, the basal area and number of trees was then reduced by 30%, following the Estonian thinning instructions. In spite of different performance in short-term prediction, both simulation combinations showed quite comparable performance in long-term projections.

The main advantage of the use of algebraic difference equations over the fixed-step increment equations is the ability to use flexible time steps. However, experience has shown that the projection intervals should not deviate too much from the time steps of the measurement data. An important constraint when using the algebraic difference equations is to avoid long-term predictions in one prediction sequence. Fig. 5 shows an example of the long-term projection of stand density in three different initial densities. A considerable variance in model predictions in comparison of observed values can be seen. This typically happens when only non-overlapping intervals have been used in the model parameter estimation. It is often advisable to use all possible intervals, but even in that case one has to be careful with long-term projections in one sequence.

4. Conclusions

This study compares the results of stand simulation using fixed interval increment functions and algebraic difference functions with variable interval lengths. To compare the flexibility of two different types of empirical model in stand-level prediction, we tested the performance of: (a) increment equations developed in the current study on the basis of interval plot data (Eqs. (4), (6), (8) and (10)), (b) algebraic difference equations calibrated on interval plot data (Eqs. (12) and (13)) and (c) algebraic difference equations developed on Estonian forest inventory data (Eqs. (1)–(3)). The model tests were carried out by comparing the projections of five stand variables (height, quadratic mean diameter, basal area, survival and volume) in different combinations.

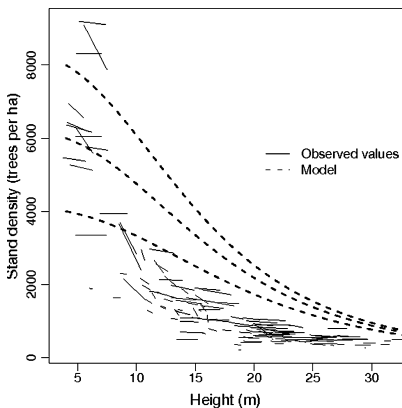


Fig. 5. The algebraic difference models prediction trajectories with three different initial states in comparison with the observed data from the Estonian network of permanent forest growth and yield monitoring plots.

The results do confirm the assumption that using different types of model for obtaining projected stand variables makes the projections differ, but not the assumption that considerable differences can be expected in projections when using different combinations of predictor variables in calculation sequences for obtaining projected variables. In this regard, the 5-year projections of dependent stand variables with simulation combinations using increment equations showed negligible difference from each other, but considerable difference from difference equations.

Stand density development is one of the most important but still complicated aspects of forest modeling. The algebraic difference models allow us to predict the average long-term stand development in accordance with a given initial state. The growth models developed in the current study predict growth by 5-year intervals and are therefore inconvenient for the end-user to apply. On the other hand, they are more flexible when taking the limiting line of self-thinning into account. The stands on interval plots used for model parametrizations have not reached the self-thinning state yet and show relatively high basal area and diameter growth. Improving the prediction abilities of these models requires longer intervals of undisturbed development.

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Modelling Stand Mean Height in Young Naturally Regenerated Stands – a Case Study in Järvselja, Estonia

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Abstract

A classic approach to obtain stand height H_{Dq} in advanced stands in Estonia has been to use regression height at the quadratic mean diameter Dq . In juvenile stands, where a considerable number of seedlings have not reached breast height, the modelling of the height distribution instead of the breast height diameter dbh distribution is more practical. Also, the field assessment methodologies differ for juvenile and advanced stands. In younger stands mean height and stem number are assessed. In advanced stands (dbh larger than 6 cm) these variables are replaced with basal area, quadratic mean diameter and regression height. This study evaluates the predictive abilities of different mean height calculation functions in various tree species in naturally regenerated stands. We analyze different young stand height calculation methods in comparison with the classical stand height H_{Dq} calculation method. Two independent sets of empirical materials were employed in our study: 27 plots from Estonian Network of Forest Research Plots (ENFRP) were used in regression analysis and three forest regeneration study areas (45 plots) at Järvselja (JS plots) were used for model validation. In the current study the r -power mean height H_r ($H_r = \sqrt[r]{(\sum h^r)/n}$ where the exponent r value 3.627 estimated on 27 ENFRP plots) was fitted to regression height H_{Dq} . We recommend using the dominant tree selection method for measuring stand height in juvenile stands. Our results indicate that the ratio of dominant trees k and stand component cluster dominant height H_k are adequate for calculating stand height in young stands as follows $H_{Dq} = a_1 \cdot H_k^{a_2} \cdot k^{a_3}$.

Key words: height distribution, mean height, dominant height, Scots pine, Norway spruce, Silver birch

Introduction

There are a number of univariate growth functions with asymptote and inflection points that are recommended for modelling the development of height over age (Kiviste 1988, Zeide 1993, Shvets and Zeide 1996). In addition, the fitted model should have biological interpretation (Vanclay and Skovsgaard 1997); however, in young stand as in this study, where height growth has not reach the inflection point, the widely used growth functions may give unrealistic height growth projections and are not suitable for height growth modelling.

Stand development predictions in time often depend on reliable height-diameter functions requiring height as the basic input variable (Temesgen and Gadow 2004). Stand height can be described in several ways: as mean-unweighted, mean-weighted, predominant, top and dominant height. Stand mean height-unweighted (or arithmetic average height) is rarely used, as its estimation requires measuring every tree height in the stand, which is possible to carry out in stands with height not more than 2–3 m (Krigul 1972). In some cases sample tree heights or tree heights from subsamples can be used for lowering the field assessment costs. Missing heights are obtained indirectly – using a suitable height-diameter relationship (e.g. Larsen and Hann 1987, Temesgen and Gadow 2004). To describe a stand's growth and yield, usually the stand dominant height is used, instead of stand average height. The advantage of dominant height is that it is relatively unaffected by thinning, when (normal) thinning operations remove the smaller trees or dying trees (Vaus 2005).

The development of stand height can be presented by using a 3- parameter, asymptotic function, such as the Chapman-Richards function (Pienaar and Turnbull 1973). Studies in Unites States have shown that stand average dominant height can be accurately predicted using a percentage of the diameter distribution, when arranged in decreasing size order (Bailey and Brooks 1994, Bailey and Martin 1996). This technique using standard inventory data, has been successfully applied to slash pine (*Pinus elliotii* Engelm.) (Bailey

and Brooks 1994) and loblolly pine (*Pinus taeda* L.) (Bailey and Martin 1996) plantations. Brooks (2004) tested this methodology and estimated the stand dominant height for young longleaf pine (*Pinus palustris* P. Mill.) plantations.

In Europe generalized height-diameter functions have been used since the 1930's. The generalized height diameter function includes both single tree level variables as individual tree heights and diameters, together with stand level variables like basal area and quadratic mean diameter (Gadow and Hui 1999, Temesgen and Gadow 2004). To calculate Lorey's mean height the stand height is weighted by the stand basal area to avoiding being affected by both natural and anthropogenic disturbances (Laar and Akça 2007).

Describing young stand development is a challenge, as growing conditions in young stands are changing rapidly. Still, it is the most crucial period for modelling or for management planning since in this period the stand properties will be set for the entire rotation period. Forest growth modelling in the Nordic and Baltic countries has focused on advanced or mature stands. Very often the growth in early stands is predicted by using the same models as for mature stands. The evaluation of young stand height thus usually leads to over- or underestimation (Huuskonen and Miina 2007).

A classic approach to obtain stand height H_{Dq} in advanced stands in Estonia has been to use regression height prediction at the quadratic mean diameter D_q . Accordingly, all tree heights are calculated using the height regression function. Depending on differences in height growth and tree ingrowth in juvenile stands, the time during which a considerable number of seedlings have not reached breast height can be very long (especially in naturally regenerated stands). Therefore, modelling of the height distribution instead of the breast height diameter (dbh) distribution is technically more advisable. Another important aspect is that the field assessment methodologies are different for juvenile and advanced stands (Siipilehto 2009). In younger stands mean height and stem number are assessed. In advanced stands (dbh larger than 6 cm) these variables are replaced with basal area, quadratic mean diameter and regression height.

More functional and realistic height projections are needed for the early stand development phase in Estonia. Height growth has only been studied for the fast-growing tree species (*Betula pendula* Roh., *Alnus incana* L. Moench., *Alnus Hybrida* A. Br., *Populus × wettsteinii* Hämet-Ahti) planted on former agricultural lands (Jõgiste *et al.* 2003, Vares *et al.* 2003). The evaluation of stand height in young stands is needed to assign to the changing requirements of forest management planning.

The aim of this paper is to evaluate the predictive abilities of different mean height calculation functions in various tree species in naturally regenerated stands. In our study we analyze different young stand height calculation methods in comparison with the classical stand height H_{Dq} calculation method.

Material and methods

Estonian Network of Forest Research Plots

The Network of Estonian Forest Research Plots (**ENFRP**) was established in 1995 (Kiviste *et al.* 2003) to provide empirical data for developing forest growth and yield models (Kiviste and Hordo 2003). The network establishment is based on the experience of Finnish studies (Gustavsen *et al.* 1988). Following the grid of ICP Forest level I monitoring plots (Karoles *et al.* 2000), the ENFRP contains 730 in 5-yearinterval re-measured sample plots, distributed with random placing in two- to ten-plot clusters over the entire land surface of Estonia (Figure 1). Most plots are in heath, mesotrophic, meso-eutrophic, and nemoral forest site types.

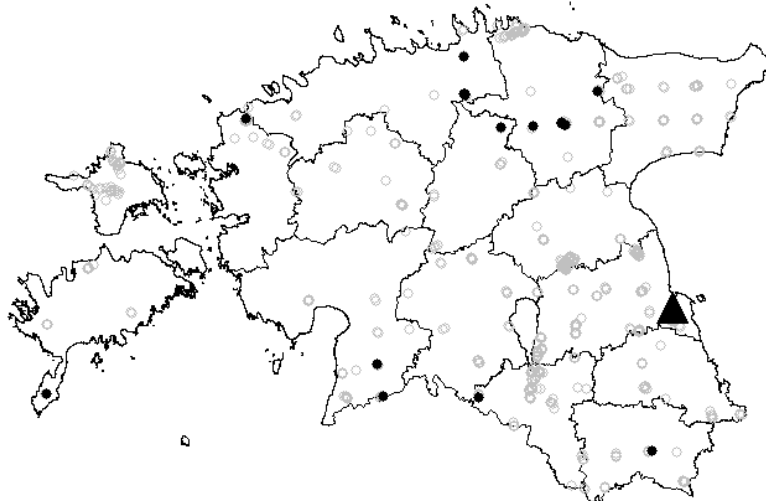


Figure 1. Spatial distribution of all ENFRP plot clusters (one cluster includes 2 to 10 plots group) across Estonia (empty circles) together with the locations of the 27 plots (filled circles) in this study. The filled triangle indicates the location of Järvelja Training and Experimental Forest Centre

The plots are circular with varying radii (15, 20, 25 or 30 meters) and each plot includes at least 100 main storey trees. Second-storey and undergrowth trees are measured in an inner circle with a radius of 8 or 10 meters depending on the main plot radius. In each plot for all trees the tree coordinates are fixed and breast height diameters are measured. In addition, the total tree height and crown length of selected sample trees (every fifth tree) are also measured (Kiviste and Hordo 2003). In Estonia the concept of stand component is used to describe different tree species forming a certain stand layer (e.g. second layer spruce). The age for different stand components is determined by the date of establishment of the stand component, which is during the first plot measurement by counting tree rings from core samples extracted from sample trees. The plots are re-measured in five-year intervals.

Table 1. Stand component data from the ENFRP plots

Tree species	Number of stand components	Min	Max	Min	Max	Number of trees	Number of sample trees	Single tree height, m		
		H_{Dq} m	H_{Dq} m	k	k			min	mean	max
all	42	4.31	13.11	0.125	0.833	1759	859	1.4	7.9	18.4
all conifers	20	4.31	11.59	0.125	0.833	722	444	1.4	6.5	16.6
all broadleaves	22	4.40	13.11	0.222	0.763	1037	415	2.9	8.9	18.4
pine	6	4.31	11.59	0.372	0.730	317	170	1.4	5.7	16.6
spruce	14	4.58	10.94	0.125	0.833	405	274	2.1	7.2	13.4
birch	15	4.40	11.26	0.282	0.763	875	356	3.0	8.9	15.8
broadleaves (birch excluded)	7	7.43	13.11	0.222	0.667	162	59	2.9	8.5	18.4

In single tree and stand level height calculations, data from 27 ENFRP plots were used which corresponded with the set criteria: 1) plot radius is greater than or equal to 14 meters; 2) maximum height of dominant trees in the main storey is less or equal to 15 meters; 3) the mean age of the main storey is less than or equal to 20 years. In the 27 selected plots, 5,125 single tree measurements (with 1,308 height measures) were distributed between 88 different stand components. The stand characteristics of the simulated plot clusters are presented in Table 1. These include 1,759 single tree measurements for 42 stand components.

Regeneration study plots at Järvelja

A series of nine study areas (JS plots) was established in 2005 in south-eastern Estonia at the Järvelja Training and Experimental Forest Center (58°25'N, 27°46'E) for study of the growth dynamics in young naturally regenerated forests.

Sample areas were divided into three different young stands and are located together in stands depending on stand size in one, three and five study groups. Nine sample areas were distributed within stands at even intervals of 50 meters. The sample plots inside the study areas were located using cluster arrangement as shown on Figure 2. Every cluster included five circular 50 m² size plots (radii = 4 m).

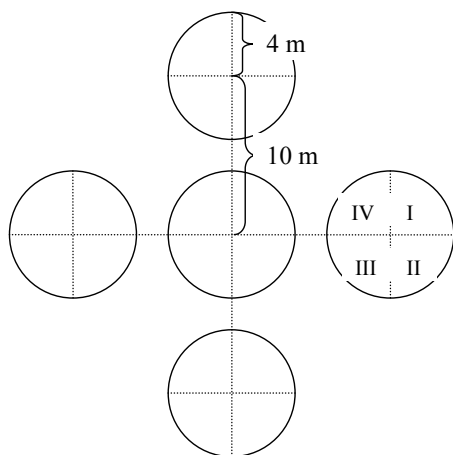


Figure 2. A design of five circular plots cluster within the study areas

The center of the middle plot in a cluster was set in the center of a study area. The other four plots were located 10 meters away to the north, south, east and west. The plot centre was marked with a metal pole. Furthermore, all plots were divided into four sectors (each 12.5 m^2) following the north-south and west-east axes. Each sector was numbered, starting from the northeast quarter.

From the center of the middle plot in the cluster, at a distance of 5, 10 and 15 meters to north, south, east and west, the depth of soil organic matter excluding moss and lichen layer was defined. Data describing site characteristics were recorded according to Löhmus's (2004) classification.

During the first four measurement occasions we measured height for all trees higher than 0.8 meters from the ground level. Beginning in 2008 all tree heights were measured starting from the ground level. The tree records at each re-measurement included sector number, tree layer, tree species and total tree height. Within each sample plot sector, three highest sample trees were selected from the dominant tree species. In addition, one sample tree was selected for every other tree species found in the sector. For each sample tree higher than 1.3 meters, dbh in two directions (to plot center direction and perpendicular), total height, the height of living crown base and height of lowest dead branch (thickness $\geq 2 \text{ cm}$, length $\geq 10 \text{ cm}$) were measured. Damages, classified according to cause and

severity, on the sample trees were recorded. In addition, tree coordinates were assessed from the center of cluster for all sample trees.

Table 2. Stand component data from Järvelja plots

Tree species	Number of stand components	Tree height, m		Number of trees
		Min	Max	
all	146	0.05	13.90	10086
all conifers	43	0.80	10.90	1819
all broadleaves	103	0.05	13.90	8267
pine	7	0.80	2.87	38
spruce	36	0.80	10.90	1781
birch	36	0.79	12.80	3973
aspen	18	0.41	13.90	2425
linden	15	0.05	7.70	912
other broadleaves	34	0.80	6.80	957

The stands were measured in July and August in 2005, and re-measured at the end of the vegetation period (September or October) in 2006, 2007 and 2008. The four different measurement periods were considered in data analyzed independently, including in total 10,086 single tree measurements distributed between 146 stand components. The general stand component data is presented in Table. 2.

Modelling

Simulation of single tree heights on the ENFRP plots

On the ENFRP plots a tree height is measured for every 5th tree; however, for simulating the JS plot establishment on ENFRP data, tree heights must be predicted for all trees. For simulation of tree height, an equation (Eq. 1) consisting of fixed and random components was applied (Padari 1999):

$$h_s = 1.3 + a \left(\frac{dbh}{dbh + b} \right)^c + \varepsilon \quad (1)$$

where h_s is simulated tree height (m), dbh is diameter at breast height (cm), a and c are model parameters estimated from sample tree data for each of 42 stand components, b is a tree species dependent constant (1.1 for pine, 1.3 for spruce, 8.0 for birch, 1.6 for ash and 4.3 for other broadleaves), ε is random variable with normal distribution $\varepsilon = N(0; SE)$, SE is residual standard error.

For estimation of parameters a and c , Eq. 1 was transformed into a linear regression equation as follows:

$$\ln(h - 1.3) = \ln(a) + c \cdot \ln \left(\frac{dbh}{dbh + b} \right) \quad (2)$$

The simulated tree heights h_s were used in following calculations as real tree height.

Sample trees selection and sample trees mean height calculations on ENFRP plots

The cluster selection system similar to the one used in JS plots was simulated for the plots from ENFRP. From each simulated sector (Figure 2) the two highest trees (regardless of species) were selected. Thus each sample plot cluster included up to 40 single tree heights. Obtained heights were grouped by stand components and for every group six different means (Eq. 3 ... Eq. 8) were calculated as cluster dominant heights for juvenile stands.

For testing the effect of using different methods in calculating cluster dominant height, the following six equations were used:

$$H_{quad} = \sqrt{\frac{\sum h_i^2}{n}} \quad (3)$$

$$H_{sqr} = \left(\frac{\sum \sqrt{h_i}}{n} \right)^2 \quad (4)$$

$$H_{arit} = \frac{\sum h_i}{n} \quad (5)$$

$$H_{cube} = \sqrt[3]{\frac{\sum h_i^3}{n}} \quad (6)$$

$$H_{geom} = \exp \left(\frac{\sum \ln(h_i)}{n} \right) \quad (7)$$

$$H_{harm} = \frac{n}{\sum \frac{1}{h_i}} \quad (8)$$

where H_{quad} is quadratic mean height, H_{sqr} is square root mean height, H_{arit} is arithmetic mean height, H_{cube} is cubic mean height, H_{geom} is geometric mean height, H_{harm} is harmonic mean height, h_i is measured tree height and n is number of trees.

Combining simulation combinations

To assess the relationship between the classical regression height (H_{Dq}) calculation method for advanced stands in Estonia and cluster dominant height in juvenile stands, we began by predicting regression height (H_{Dq}) for simulated plot clusters as follows:

$$H_{Dq} = 1.3 + a \left(\frac{Dq}{Dq + b} \right)^c \quad (9)$$

where H_{Dq} is regression height of the tree with the quadratic mean diameter for stand component (m), Dq is stand component quadratic mean diameter (cm), a and c are regression coefficients (Eq. 2) and b is a tree species dependent constant (Eq. 1). The estimates of parameters a and c were re-estimated for the simulated data.

On a stand level four different regression equations (Eq. 10 ... Eq. 13) were used to analyze H_{Dq} predictions in case of six different means for cluster dominant mean height (Eq. 3 ... Eq. 8)

$$H_{Dq} = a_1 + a_2 \cdot H_k + a_3 \cdot k \quad (10)$$

$$H_{Dq} = a_1 + a_2 \cdot H_k + a_3 \cdot k + a_4 \cdot H_k \cdot k \quad (11)$$

$$H_{Dq} = a_1 \cdot H_k^{a_2} \cdot k^{a_3} \quad (12)$$

$$H_{Dq} = a_1 \cdot H_k^{a_2} \cdot k^{a_3} + a_4 \cdot H_k \cdot k \quad (13)$$

where H_{Dq} is stand component regression height (m), H_k stand component cluster dominant height (arithmetic, quadratic, cubic, harmonic, square root or geometric), k is ratio of number of sample trees to total number of trees, and a, b, c, d are model parameters.

The first two regression equations (Eq. 10 ... Eq. 11) are linear whereas the two last (Eq. 12 ... Eq. 13) are nonlinear. According to these functions lm and nls were used for parameter estimations with R software (Crawley 2007).

The simulation was carried out by combining the four different model forms (Eq. 10 ... Eq. 13) with six different transformations of cluster dominant height calculations (Eq. 3 ... Eq. 8) for seven different tree species or tree species groups.

Descriptive statistics of 42 stand components from the 27 ENFRP plots are presented in Table 1.

For each regression equation (Eq. 10 ... Eq. 13) and tree species or tree species group, the best performing cluster dominant height calculation combination were selected.

Model validation on Järvelja data

The selected 28 equations were used in validation of JS plots and were used in the mean height calculations for each stand component on JS data (see Table 2).

The obtained stand component's mean height calculated from cluster dominant height H_k and ratio k were intended for comparison with the corresponding regression height H_{Dq} on JS data. On the Järvelja plots, the tree heights are measured for all the trees, but the diameters are measured only for selected sample trees; therefore, it is not possible to compute mean height H_{Dq} directly. For this study, mean height H_{Dq} was considered equivalent to r -power mean of tree heights H_r (Eq. 14)

$$H_r = \sqrt[r]{\frac{\sum h_i^r}{n}} \quad (14)$$

where H_r is r -power mean height (m), r is exponent term, n is number of measured tree heights, h_i is single tree height (m).

The relationship between r -power mean height and regression height was studied on the basis of ENFRP plots. Optimal exponent term r was estimated for each tree species or tree species group.

The r values estimated on ENFRP plots were used for calculating r -power mean height as a substitute for the missing regression height for JS data. For evaluating simulation combinations, their predictions were compared with the corresponding r -power mean heights (H_r) using the paired t-test. Three criteria were set to better distinguish between simulation combinations: 1) the quadratic mean difference (SE) is less than 0.8 m, 2) the mean difference is less than 0.10 m and 3) p-value from t-test of differences exceeds 0.05.

In addition a test was carried out on JS data to clarify the sample tree selection preferences for selected stand mean height models. Five different sample trees selection methods were used, where:

- from each plot sector the two tallest trees were selected (N_{st2});
- from each plot sector the three tallest trees were selected (N_{st3});

- from each plot sector the four tallest trees were selected (N_{st4});
- from each plot sector the six tallest trees were selected (N_{st6});
- the sample trees were selected as in JS field measuring (N_{streal}).

Results and discussion

This study presents the stand height prediction functions which show the closest relation to the commonly used regression height H_{Dq} for naturally regenerated young stands employing the cluster dominant stand component height H_k and the ratio k between number of selected dominant trees and total tree number as predictor variables. The regression height H_{Dq} is not directly applicable to stands where the trees have not reached breast height (Siipilehto 2009). An alternative approach based on single tree height distribution is offered for obtaining the r -power mean height (H_r) as a stand height in young stands being the closest to classically used stand height (H_{Dq}).

Tree selecting simulation on ENFRP plots according to the cluster selection method used in field sampling in JS plots resulted in a total of 1,759 single tree samples divided among 42 different stand components. These selected trees were used for model selection for three main tree species (Scots pine, Norway spruce and silver birch) and four tree species groups (all trees together, all conifers together, all broadleaves together, and all broadleaves together excluding birch (Table 1)). The dataset covered a range of tree heights from 1.4 m to 18.4 m.

Model selection and parameter estimation

All combinations of four regression equations (Eq. 10 ... Eq. 13), six mean height equations (Eq. 3 ... Eq. 8) and seven tree species or tree species groups were used for modelling regression height H_{Dq} with predictor variables H_k and k on ENFRP data. For the 28 best calculation combinations (CN), fit statistics including adjusted determination coefficient (R^2), residual standard error (SE) value and parameter estimates on ENFRP data are presented in Table 3.

Table 3. Best performing models by tree species and model shape. CN – combination number

CN	Eq. no.	Tree species	Number of stand components	Mean height	R ²	SE, m	Regression constants			
							a ₁	a ₂	a ₃	a ₄
1	(10)	all	42	H _{arit}	0.943	0.573	-0.2613	0.9100	1.4112	-
2	(10)	all conifers	20	H _{arit}	0.934	0.618	0.2441	1.0048	-0.3801	-
3	(10)	all broadleaves	22	H _{arit}	0.978	0.340	-1.2748	0.9264	3.0596	-
4	(10)	pine	6	H _{arit}	0.999	0.122	-0.8980	0.9952	1.3909	-
5	(10)	spruce	14	H _{arit}	0.887	0.725	0.6870	0.9657	-0.4930	-
6	(10)	birch other	15	H _{arit}	0.985	0.293	-0.9602	0.9128	2.5027	-
7	(10)	broadleaves except birch	7	H _{arit}	0.979	0.368	-0.9169	0.8269	4.8750	-
8	(11)	all	42	H _{arit}	0.962	0.475	3.6449	0.4268	-5.9945	0.9130
9	(11)	all conifers	20	H _{arit}	0.938	0.618	3.6089	0.4777	-5.6548	0.8019
10	(11)	all broadleaves	22	H _{arit}	0.983	0.304	1.5968	0.6166	-2.7526	0.6234
11	(11)	pine	6	H _{arit}	1.000	0.039	3.5549	0.1745	-5.7712	1.2925
12	(11)	spruce	14	H _{arit}	0.915	0.660	9.5843	-0.4068	-13.6933	1.9932
13	(11)	birch other	15	H _{arit}	0.988	0.281	0.8598	0.7149	-1.2718	0.4119
14	(11)	broadleaves except birch	7	H _{arit}	0.990	0.297	3.9534	0.2991	-4.2968	0.9769
15	(12)	all	42	H _{arit}	0.968	0.559	1.1917	0.9339	0.0933	-
16	(12)	all conifers	20	H _{arit}	0.996	0.611	0.9861	1.0005	-0.0369	-
17	(12)	all broadleaves	22	H _{arit}	0.897	0.320	1.1549	0.9670	0.1609	-
18	(12)	pine	6	H _{arit}	0.990	0.108	1.0536	1.0023	0.1429	-
19	(12)	spruce	14	H _{arit}	0.985	0.722	1.0920	0.9557	-0.0354	-
20	(12)	birch other	15	H _{arit}	0.896	0.284	1.1262	0.9672	0.1396	-
21	(12)	broadleaves except birch	7	H _{arit}	0.841	0.373	1.5938	0.8562	0.2204	-
22	(13)	all	42	H _{arit}	0.957	0.511	0.6094	0.9250	-0.2921	0.6176
23	(13)	all conifers	20	H _{arit}	0.980	0.586	0.6293	0.9782	-0.2904	0.4744
24	(13)	all broadleaves	22	H _{arit}	0.888	0.315	0.7905	0.9657	-0.0376	0.4020
25	(13)	pine	6	H _{arit}	0.984	0.115	0.5683	1.0054	-0.2302	0.5526
26	(13)	spruce	14	H _{arit}	0.963	0.721	0.7635	0.9179	-0.2512	0.4270
27	(13)	birch other	15	H _{arit}	0.884	0.286	0.7821	0.9664	-0.0602	0.3738
28	(13)	broadleaves except birch	7	H _{arit}	0.800	0.315	1.0127	0.7152	-0.1574	0.7653

The first two linear regression equations (Eq. 10 and Eq. 11) might not give realistic predictions for stand early development (H_k less than four meter tree height); however, nonlinear regression equations (Eq. 12 and Eq. 13) start always from zero and therefore we can assume their near reality prediction even in case of very small trees (H_k less than breast height 1.3 m).

It is important to note that of the six different mean height calculations, only the arithmetic mean height (H_{arit}) seems to work with all equations and tree species. The cubic

mean height (H_{cub}) gave the poorest fit results in mean height calculation combinations. On the other hand, using H_{arit} as the sample trees height distribution has to the least effect on stand mean height H_k calculations versus other mean heights.

According to the results presented in Table 3, the residual standard errors (SE) are as follows: Eq. 10: 0.12–0.73 m, Eq. 11: 0.04–0.66 m, Eq. 12: 0.11–0.72 m and Eq. 13: 0.12–0.72 m. Norway spruce showed significantly higher residual standard errors (ranging from 0.66–0.73 m) than SE values for other tree species (the highest SE value is 0.37 m). The poor fit of spruce can be explained by the irregular height distribution in young stands caused by new spruce regeneration coexisting with advanced regeneration.

Calculation of r -power mean height for juvenile stands

Based on the data from ENFRP plots, the regression height H_{Dq} and r -power mean height H_r for r values from 3.0 to 4.0 by 0.1 were calculated according to Eq. 14 for all stand components. Relationships between average difference of ($H_r - H_{Dq}$) and exponent r for different tree species and tree species groups are presented in Figure 3.

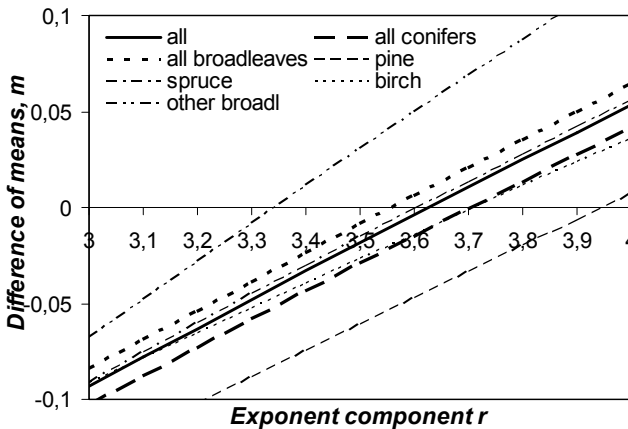


Figure 3. The average difference between regression height of the tree with the quadratic mean diameter and r -power mean height on the data of ENFRP plots depending on exponent r

Estimations of exponent term r for different tree species or tree species groups were chosen where the difference between regression height H_{Dq} and r -power mean height was zero (Figure 3) and are presented in Table 4. The exponent r estimations vary depending on tree species. For Scots pine and silver birch the estimated r values are higher than for Norway spruce. This can be explained by different tree species dependent height distribution and height-diameter relationships. At the same time the difference between regression height H_{Dq} and r -power mean height is the lowest for Scots pine.

Table 4. Comparison results for mean heights (regression height of the tree with the quadratic mean diameter and exponent mean height) with paired t-test

Tree species	Exponent component r	Quadratic mean difference, m	Mean of the differences	95% confidence intervals	
				lower	higher
all	3.627	0.153	-0.000024	-0.048	0.048
all conifers	3.706	0.183	0.000050	-0.088	0.088
all broadleaves	3.558	0.120	-0.000045	-0.054	0.054
pine	3.949	0.078	0.000000	-0.089	0.089
spruce	3.608	0.210	-0.000071	-0.126	0.126
birch	3.712	0.118	-0.000067	-0.068	0.068
other broadleaves	3.343	0.124	0.000143	-0.124	0.124

Evaluation of selected model combinations with dominant tree selection on JS data

For evaluation of 28 selected model combinations (see Table 3) an independent JS dataset was employed. The total number of individual tree heights used for the height prediction comparison with r -power mean height was 10,086 divided among 146 stand components. The JS dataset covered a range of tree heights from 0.05 m to 13.90 m (Table 2).

For all 146 JS stand components H_{Dq} was predicted using different simulation combinations (CN from Table 3) according to: 1) tree species specific parameter combinations CN (Eq. 10) = 4, 5, 6, 7; CN (Eq. 11) = 11, 12, 13, 14; CN (Eq. 12) = 18, 19, 20, 21 and CN (Eq. 13) = 25, 26, 27, 28, 2) broadleaves and conifers group specific

parameter combinations CN (Eq. 10) = 2, 3; CN (Eq. 11) = 9, 10; CN (Eq. 12) = 16, 17 and CN (Eq. 13) = 23, 24 and 3) generalized parameter combinations CN (Eq. 10) = 1; CN (Eq. 11) = 8; CN (Eq. 12) = 15 and CN (Eq. 13) = 22. The r -power mean height (Eq. 14) was calculated following the model combinations for every obtained stand component H_{Dq} as a reference height for t-test comparison. Five different dominant height sample tree selection methods (see Table 5) were applied to all simulation combinations and are presented in Tables 6, 7 and 8).

Table 5. Sample tree totals by selection method

Tree species	Number of trees	Number of sample trees				
		N_{st2}	N_{st3}	N_{st4}	N_{st6}	N_{streal}
all	10086	1351	1956	2494	3393	2494
all conifers	1819	330	492	621	798	663
all broadleaves	8267	1021	1464	1873	2595	1831
pine	38			2	6	23
spruce	1781	330	492	619	792	640
birch	3973	625	881	1090	1461	989
aspen	2425	322	468	601	810	560
linden	912	20	31	55	103	77
other broadleaves	957	54	84	127	221	205

Table 6. Standard errors between r -power mean height (H_r) and estimated mean height. CN indicates the model combination according to Table 4. *Bold* indicates the differences that are less than 0.8 m

CN	SE				
	N_{st2}	N_{st3}	N_{st4}	N_{st6}	N_{streal}
1	0.581	0.541	0.501	0.484	0.481
8	1.856	1.704	1.621	1.446	1.521
15	0.517	0.490	0.452	0.408	0.412
22	1.685	1.387	1.154	0.702	0.630
2, 3	0.797	0.768	0.693	0.707	0.770
9, 10	1.250	1.129	1.055	0.933	0.932
16, 17	0.700	0.598	0.493	0.444	0.482
23, 24	0.915	0.764	0.580	0.432	0.453
4...7	0.876	0.856	0.880	1.126	1.087
11...14	2.400	2.219	2.021	1.727	1.871
18...21	0.790	0.677	0.557	0.501	0.563
25...28	1.169	1.011	0.874	0.681	0.647

Table 7. Average difference (m) between r -power mean height (H_r) and estimated mean height (H_{Dq}). CN indicates the model combination according to Table 3. *Bold* indicates the differences that are less than 0.1 m

CN	Average difference ($H_r - H_{Dq}$), m				
	N_{st2}	N_{st3}	N_{st4}	N_{st6}	N_{streal}
1	0.291	0.233	0.264	0.236	0.150
8	1.513	1.181	0.921	0.368	0.575
15	0.271	0.200	0.200	0.095	0.042
22	1.017	0.711	0.572	0.297	0.288
2, 3	-0.054	-0.086	-0.018	0.026	-0.142
9, 10	0.882	0.647	0.494	0.127	0.204
16, 17	0.120	0.042	0.037	-0.058	-0.121
23, 24	0.395	0.245	0.194	0.054	0.009
4...7	0.134	0.145	0.249	0.423	0.240
11...14	1.729	1.466	1.218	0.768	0.935
18...21	0.178	0.125	0.137	0.087	0.017
25...28	0.740	0.557	0.503	0.359	0.327

Table 8. T-test p-values between r -power mean height (H_r) and estimated mean height. *CN* indicates the model combination according to Table 3. *Bold* indicates p-values more than 0.05

CN	T-test p-values				
	N _{st2}	N _{st3}	N _{st4}	N _{st6}	N _{streal}
1	6e-09	6e-07	7e-11	1e-09	0.0001
8	<2e-16	<2e-16	1e-12	0.0027	3e-06
15	1e-09	2e-06	1e-07	0.0060	0.2139
22	4e-13	1e-09	2e-09	2e-07	6e-09
2, 3	0.4734	0.2157	0.7612	0.6736	0.0249
9, 10	<2e-16	3e-12	2e-08	0.1158	0.0088
16, 17	0.0622	0.4338	0.3965	0.1268	0.0021
23, 24	1e-06	0.0003	9e-05	0.1449	0.8154
4...7	0.0974	0.0597	0.0010	6e-06	0.0072
11...14	<2e-16	<2e-16	2e-14	1e-07	2e-10
18...21	0.0135	0.0387	0.0043	0.0417	0.7115
25...28	1e-14	3e-11	5e-13	3e-11	7e-11

The comparison results (Tables 6, 7 and 8) between r -power mean height and predicted H_{Dq} values showed better performance with model combinations where the third (Eq. 12) equation was used. The tree species or species group wise analysis indicated that there are no considerable differences in predictions when using species specific or general model combinations in predicting stand mean height. Following the parsimonious principle (Burkhart 2003) to select the recommended simulation combination for predicting stand component mean height closest to regression height H_{Dq} in juvenile stands:

$$H = 1.192 \cdot H_k^{0.934} \cdot k^{0.093} \quad (16)$$

where H_k is arithmetic mean of cluster selected dominant trees, k is ratio of number of sample trees to total number of trees

For all measured tree heights the 3.627-power mean is preferable:

$$H = \sqrt[3.627]{\frac{\sum H_i^{3.627}}{n}} \quad (17)$$

where H is stand component mean height (m), n is number of measured tree heights, h_i is single tree height (m).

It is quite evident and expected that with the higher number of sampled trees the stand dominant height predictions are better. However, we must be careful when comparing the stand mean height predictions between different sample tree selection methods, because in r -power mean height calculations the N_{st2} sampling method was used. The analysis of several sample tree selection methods revealed positive tendencies in species dependent sampling when comparing species independent tree sampling to dominant stand mean height prediction. The species dependent cluster selection method applied in ENFRP plots compared favorably against the real selection on JS plots, where in addition to the two highest sample trees from dominating species one tree was sampled from each co-dominating species in a particular plot sector, resulting in better prediction with lower sample tree number.

Due to natural regeneration, in stands with high spatial variation of the trees in each plot the tree sampling must take this variation into account. Otherwise, the selection might not reflect reality and the predictions will be biased. An example of such selection is presented on Figure 4 where Norway spruce stand mean height calculations based on two tree sampling N_{st2} are underestimated versus using higher sample tree numbers. This indicates that for stands where different species are present and their spatial arrangement varies, the cluster dominant height can become lower than mean height of the particular stand component.

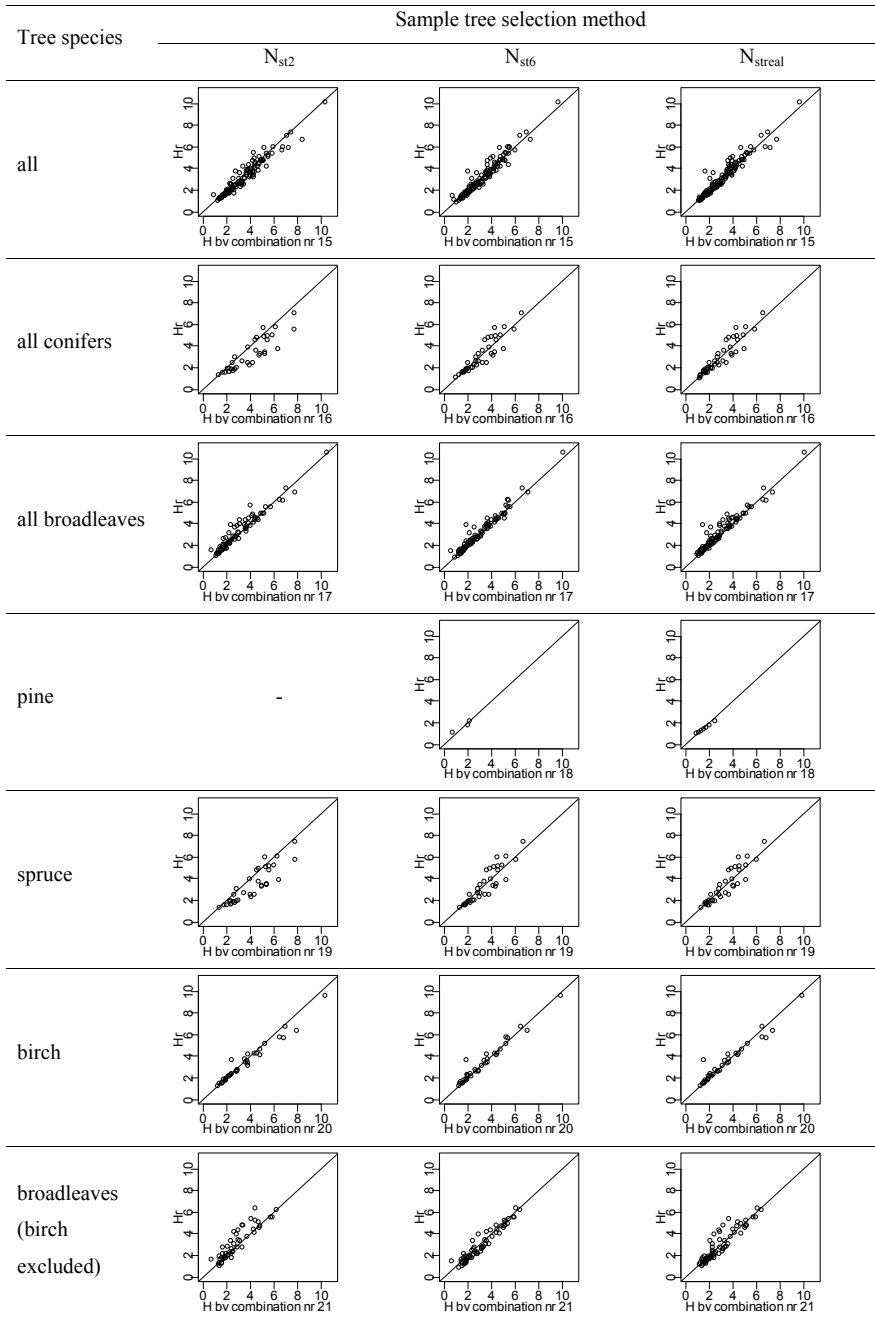


Figure 4. r -power mean height (H_r) and estimated stand mean height (H_k) for different tree species and tree species groups depending on sample tree selection method. The line represents a relationship between H_r and H_{Dq} predictions of 1:1

Conclusions

Due to missing breast height diameter data in juvenile stands, it is reasonable to use tree height distribution-based stand mean height instead of classically used regression height (H_{Dq}). In this study the r -power mean height H_r (Eq. 14) was fitted to regression height H_{Dq} and the exponent r value 3.627 was estimated on 27 ENFRP plots.

We recommend using the dominant tree selection method (where the two highest trees are measured per 12.5 m²) for measuring stand height in juvenile stands. Following the dominant tree selection method and based on our results Eq. 12 is adequate for calculating stand height in young stands (estimated model parameters are presented in Table 3).

The species dependent cluster selection method shows better prediction for lower sample tree numbers when in addition to the two highest sample trees from dominating species a single tree is sampled from each co-dominating species on a plot.

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МОДЕЛИРОВАНИЕ СРЕДНЕЙ ВЫСОТЫ МОЛОДЫХ НАСАЖДЕНИЙ НА ПРИМЕРЕ ЛЕСНИЧЕСТВА ЯРВСЕЛЬЯ, ЭСТОНИЯ

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Резюме

Классическим подходом предсказания роста насаждений в Эстонии является средняя высота (регрессионная высота) со средним квадратичным диаметром H_{Dq} в обобщенной функции высоты и диаметра. В молодняках, имеющих естественное происхождение, где значительное количество саженцев ещё не достигло высоты груди, вместо моделирования распределения диаметра более практичным является моделирование высоты. Кроме того, методы измерения среднего роста насаждений в лесу для саженцев и молодых насаждений отличаются. В молодняках с диаметром менее 6 см оценивается средняя высота насаждений и количество деревьев. В то время как в молодняках с диаметром более 6 см используются сумма площадей поперечных сечений насаждения, регрессионная высота и средний квадратичный диаметр деревьев. В ходе исследования были оценены прогностические возможности различных методов калькуляции средней высоты для разных пород деревьев в насаждениях восстанавливающегося естественном путём. Были сравнены различные методы вычисления средней высоты насаждений классическим методом. В нашем исследовании были использованы две независимые выборки эмпирических данных: 27 участков эстонской сети лесных пробных площадей (ENFRP) были использованы для регрессионного анализа, а данные с трёх зон (45 пробных площадей) в Ярвселья, где проводится исследование лесовосстановления, были использованы для проверки модели. В данной работе, r -степенная средняя высота H_r (функция 14) была оценена для 27 участков эстонской сети лесных пробных площадей (ENFRP) и сравнена с регрессионной высотой H_{Dq} . Для измерения высоты молодых насаждений (диаметр менее 6 см) можно рекомендовать доминирующие деревья изучаемых секторов наилучшие результаты дала функция 12.

Ключевые слова: распределение высоты, средняя высота, доминирующая высота, сосна обыкновенная, ель обыкновенная, берёза повислая

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1999-2000 Eesti Põllumajandusülikooli Üliõpilasesindus, kultuuritoimkonna esimees;

1998-1999 Tartu Arenduskeskuse Külalistemaja,
klienditeenindaja.

Teaduskraad

2005 Eesti Põllumajandusülikool, metsateaduse
magister metsamajanduse erialal, magistritöö
“Metsaökosüsteemide dünaamika kirjeldamine ja
kasutamine metsade majandamise kavandamisel”.

Erialane enesetäiendamine

2008 Rahvusvaheline doktorantide kursus “Mitmekülge
metsanduse ökoloogia, metsakasvatus ja
metsamajandus”. Kursuse korraldaja Kopenhaageni
Ülikool, Kopenhaagenis, Taanis;

2008 Kursus “Metsakorraldus ja metsade mitmekülgne
kasutamine”. Kursuse korraldaja Eesti Maaülikool,
Tartu, Eesti;

2007 Tudeerimine Helsingi Ülikooli metsaökoloogia
osakonnas, Soomes;

2006 Kursus “Metsa uuendamine boreaalsete ja laialehiste
lehtpuumetsade võondis”. Kursuse korraldaja Rootsi
Põllumajandusteadusteülikool, Alnarpis, Rootsis;

2000 Kursus “Metsandus maailmas”. Kursuse korraldaja Eesti
Põllumajandusülikool, Tartu, Eesti;

1999 Kursus “Metsaökosüsteemide majandamine”.
Kursuse korraldaja Biosfääri Kaitseala Hiiumaa Keskus,
Hiiumaa, Eesti;

Juhendatud magistritööd

2007 Merle Hämäläinen, M.Sc.
2007 Relika Kaer, M.Sc.

Teadustöö põhisuunad

Metsaökosüsteemide pikaajaline dünaamika, looduslike ja inim põhjuslike
häiringute mõju metsasuktsessioonile, looduslike häiringuid jälgendavate
võtete kasutamine metsakasutuse ja looduskaitse kavandamisel.

Keelteoskus Eesti, inglise, vene

LIST OF PUBLICATIONS

Articles in peer-reviewed journals

- Padari, A., Metslaid, S., **Kangur, A.**, Sims, A., Kiviste, A. 2009: Modelling stand mean height in young naturally regenerated stands – a case study in Järvelja in Estonia. *Baltic Forestry*, 15(2), xx-xx (Accepted manuscript 15. 06. 2009)
- Sims, A., Hordo, M., **Kangur, A.**, Kiviste, K., Jõgiste, K., Gadow, K.v. 2009: Tracking disturbances induced changes in stand development on irregular measurement intervals in the Järvelja forest experiments. *Baltic Forestry*, 15(2), xx-xx (Accepted manuscript 15. 06. 2009)
- Shorohova, E., Kuuluvainen, T., **Kangur, A.**, Jõgiste, K. 2009: Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science*, 66(2), 1 - 20.
- Kangur, A.**, Sims, A., Jõgiste, K., Kiviste, A., Korjus, H., Gadow, K.v. 2007: Comparative modeling of stand development in Scots pine dominated forests in Estonia. - *Forest Ecology and Management*, 250, 109 - 118.
- Jõgiste, K., Kuuluvainen, T., **Kangur, A.** 2007: Disturbances at multiple scales as the basis of forest ecosystem restoration and management. Introduction. – *Forest Ecology and Management*, 250, 1 - 2.
- Korjus, H., Sims, A., **Kangur, A.**, Kaar, E., Kiviste, A. 2007: Forest growth dynamics on abandoned oil shale quarries on the basis of permanent plot data. - *Miškininkysté*, 61(1), 24 - 29.
- Kangur, A.**, Korjus, H., Jõgiste, K., Kiviste, A. 2005: A conceptual model of forest stand development based on permanent sample-plot data in Estonia. – *Scandinavian Journal of Forest Research*, 20, 94 - 101.
- Kangur, A.**, Jõgiste, K., Korjus, H. 2004: Kõpu poolsaare riigimetsa säästev majandamine ökosüsteemide väärtushinnangute skooringmeetodi alusel. [Sustainable management of state-owned forests on Kõpu peninsula based on the ecosystem value evaluation method.] - *Metsanduslikud uurimused /Forestry Studies*, 40, 110 - 123.

Articles in proceedings

- Vodde, F., Barrenada, E., Laumets, S., **Kangur, A.**, Jõgiste, K. 2002: Ecosystem management plan on the Kõpu Peninsula: methodological considerations. [Ökosüsteemide majandamise kava Kõpu poolsaarel: metodoloogilised kaalutlused]. *Transactions of the Faculty of Forestry, Estonian Agricultural University*, 35: 93 - 100.

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- Köster, K.; **Kangur, A.**; Hari, P.; Jõgiste, K. 2008: Test in Estonia at the southern border of the boreal zone. In: Hari, P.; Kulmala, L. (Toim.). *Boreal forest and climate change*, Springer, 468-471.

Editorial work

- Korjus, H., **Kangur, A.**, Aavik, A. (Ed). 2008: Metsade looduslikkuse taastamine. – *Metsahoii sihtasutus, Halo Kirjastus*, 128 p.
- Jõgiste, K., Kuuluvainen, T., **Kangur, A.** (Ed). 2007: Disturbances at multiple scales as the basis of forest ecosystem restoration and management. Special issue. – *Forest Ecology and Management*, 250.
- Kangur, A.** (Ed). 2004: Natural disturbances and ecosystem-based forest management: proceedings of the international conference: Tartu, Estonia, 27-29 May 2004. – *Transactions of the Faculty of Forestry, Estonian Agricultural University*, 37, 55 p.

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- Kangur, A.**, Hordo, M., Sims, A., Jõgiste, K., Kiviste, A., Hari, P. 2007: Growth patterns from different generations of Scots pine dominated forests in Estonia: methodological considerations. – In: *Climate change impacts on boreal forest disturbance regimes, Disturbance dynamics in boreal forest, VI international conference, Fairbanks, Alaska, 30 May – 2 June, Conference program & abstracts*, p 17.
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Popular science articles

- Belova, O., **Kangur, A.** 2008: VII International Workshop of SNS Network Natural Disturbance Dynamics Analysis for Forest Ecosystem Management 'Mixed Forest Disturbances in Boreal and Temperate zone'. – *Baltic Forestry (Chronicle)*, 14(2), 216-217.
- Kangur, A.**, Jõgiste, K. 2007: Muljeid Alaska kliimakonverentsist ja metsadest. – *Eesti Mets*, 4, 44-47.
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- Jõgiste, K., **Kangur, A.**, Laumets, S. 2002: Uudne idee – metsade ökosüsteemne majandamine. – *Eesti Mets*, 3, 18-21.