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Models of individual tree mortality for trembling aspen, lodgepole pine, hybrid spruce and subalpine fir in northwestern British Columbia



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Preface

This thesis was initiated in the summer of 2005 when I was employed to carry out field work for the project: *Modelling individual tree mortality for northern mixed-species stands* (FSP-project number Y061012) by the Department of Forest Sciences at the University of British Columbia. The project was funded by the Forest Science Program which is administered by the BC Ministry of Forests and Range (<http://www.for.gov.bc.ca/forsci/>).

After the field season I was given the opportunity to carry out data analyses and report the results in my M.Sc. thesis at the Swedish University of Agricultural Sciences (SLU). Thus, this thesis is a further development of the original project as a model evaluation was added.

Dr. Rasmus Astrup (Bulkley Valley Centre for Natural Resources Research & Management) has been my main supervisor. He supervised field work and has offered valuable advice both during different steps of analyses and the writing process. I am very grateful for his big commitment to this project and for the opportunity to use the FSP-project for this thesis. He has been very patient and supportive through the whole process.

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Sammanfattning

Naturlig avgång på grund av trängsel är en viktig process för den skogliga successionen. Generellt är förmågan hos modeller för skogssimulering att göra exakta prognoser nära relaterad till hur väl de hanterar självgallring. Att hitta en lämplig metod för att modellera självgallring har ofta visat sig vara en svår utmaning. Syftet med detta examensarbete var att testa en metod på vuxna träd (DBH > 5cm) som tidigare har använts för att modellera självgallring hos plantor med gott resultat. Basmodellen skattar sannolikheten för att ett enskilt träd ska dö på grund av självgallring som en funktion av de senaste årens diametertillväxt. Dessutom testades om självgallringsmodellerna potentiellt förbättrades genom att inkludera trädstorleken som oberoende variabel.

Det utvecklades självgallringsmodeller för fyra olika trädslag: asp (*Populus tremuloides* Michx.), contortatall (*Pinus contorta* Dougl. ex Loud. var. *latifolia*), hybridgran (hybrider mellan vitgran (*Picea glauca* (Moench) Voss) och Engelmann-gran (*Picea engelmannii* Parry ex Engelm.)) och klippgran (*Abies lasiocarpa* (Hook.) Nutt.). Modellernas parametrar skattades med en maximum-likelihood metod från fältdata. Data insamlades i 16 bestånd i den sub-boreala gran zon i nordvästra British Columbia och består av totalt 337 levande och 345 nyligen döda träd. Självgallringsmodellerna testades i SORTIE-ND, en trädvis och avståndsberoende skogsproduktionsmodell. SORTIE-ND simuleringar av rena likåldriga bestånd jämfördes med simuleringar gjorda med en ofta använd beståndsbaserad skogsproduktionsmodell. Dessutom jämfördes SORTIE-ND simuleringar för permanenta provytor i olikåldriga blandbestånd med uppmätt utveckling på dessa provytor.

Genom att inkludera individuell trädstorlek i basmodellen uppnåddes bättre anpassning till fältdata. Avgångsriskerna vid låg tillväxt var minst för medelstora träd för alla trädslag förutom klippgran. För detta trädslag minskar avgångsriskerna vid låg tillväxt kontinuerligt med ökad trädstorlek. Detta är en konsekvens av de enskilda trädslagens karakteristika.

Självgallringsmodellerna bidrog till realistisk avgång i båda likåldriga och komplexa bestånd. Det är dock uppenbart att självgallringsmodellerna är väldigt beroende av de underliggande tillväxtmodellerna och modeller som uppskattar den stokastiska avgången i ett bestånd. Modellernas avvikelser är relaterade till över- eller underskattning av tillväxten och orealistiska nivåer på den stokastiska avgången.

Den testade metoden är ett relativt enkelt sätt att härleda och estimeras parametrar till en tillväxtbaserad självgallringsmodell från fältdata. Dessutom är data relativt enkla att erhålla.

Abstract

Density dependent mortality is an important process in forest succession. The overall predictive abilities of forest simulation models are closely related to their ability to predict mortality. Finding appropriate methods for modelling mortality have often proved to be a difficult challenge. The objective of this study was to test a method on adult trees, which was previously used for modelling density dependent mortality for saplings with good results. In the basic model mortality is predicted as a function of recent diameter growth. It was also tested if incorporating tree size into the mortality model improved it.

Models were developed for four species: trembling aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*), hybrid spruce (a complex of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The models were parameterized from field data using a maximum-likelihood method. Field data was gathered from 16 stands in the Sub-Boreal Spruce Zone in northwestern British Columbia and comprised of 337 live and 345 recently dead trees in total. The mortality models were tested by incorporating them into the individual tree, spatially explicit forest simulation model SORTIE-ND. SORTIE-ND simulations of single species even-aged stands were compared to simulations of a commonly used stand level simulation model. Furthermore, SORTIE-ND simulations of permanent sample plots in mixed species uneven-aged stands were compared to remeasurements of the plots.

It was determined that incorporating tree size into the mortality models gave better fits to the field data. Tolerance to low growth decreases to a minimum at intermediate trees size for all species except for subalpine fir, where it decreases and remains low as trees growth larger. This is probably an effect of the ontogenetic characteristics of the individual species.

Testing the mortality models in SORTIE-ND showed that they contribute to realistic thinning patterns in simulations of both pure even-aged stands and complex stands. However, it was evident that the performance of the mortality models is highly dependent on the underlying growth models as well as mortality models accounting for random mortality. Discrepancies in modelling results were linked to over- and underestimation of growth or inappropriate random mortality rates.

Overall the tested method provides a straight forwards approach to parameterizing growth based mortality models from field data which is relatively easy to obtain.

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Introduction

Background

Forest simulation models provide essential support for forest management. Silviculture and harvest planning, wildlife management and landscape ecological planning rely on accurate decision support tools to make forecasts at different temporal and spatial scales (e.g. Messier *et al.* 2003, Korzukhin *et al.* 1996). Traditional growth and yield models, in particular yield tables, have been widely used in forest management for more than a century (Vanclay 1994, Messier *et al.* 2003). With the implementation of management paradigms such as sustainable forest management, focus has been shifted to modelling tools that go beyond timber yields by exploring the succession and structural dynamics of forest ecosystems. Forest ecologists have been developing and utilizing such models extensively for research purposes (Dixon *et al.* 1990, Botkin 1993, Messier *et al.* 2003). The need for modelling tools that predict timber yields in conjunction with other forest attributes have led to considerable efforts from model developers to construct models more applicable to the new forest management paradigms (e.g. Coates *et al.* 2003, Welham *et al.* 2002).

By definition a model is a simplified representation of reality (Vanclay 1994, Grant *et al.* 1997, Vanclay and Skovsgaard 1997). A forest simulation model thus describes one or several aspects of a forest ecosystem, which is often highly complex both in terms of structure and dynamics (Oliver and Larson 1997, Kimmins 2005). The model may consist of many mathematical models that each describes an aspect of the ecosystem (growth, mortality, regeneration, nutrient cycling etc.). Mathematical models are very useful in forest simulation modelling as they in a concise and precise way describe and quantify response variables of interest (Hilborn and Mangel 1997). Over time, the complexity and the predictive abilities of forest simulation models have evolved as a consequence or in conjunction with advances in other fields such as computer technology, mathematics and forest ecology (Vanclay 1994). Still, models are limited by both available data and the understanding of how forest ecosystems work. Tree mortality, which is the focal point of this study, is one of the most complex and least understood forest ecosystem processes and is often poorly described in forest simulation models (Hawkes 2000).

General approaches in forest simulation modelling

Forest simulation models are often classified as empirical or process-based models (Mohren and Burkhart 1994, Vanclay 1994, Messier *et al.* 2003). Yield tables and curves are typical examples of empirical models. They describe the statistical relationship between variables of interest, e.g. volume production as a function of age for a given tree species. The underlying processes are not taken into consideration. Thus, development of an empirical model depends on empirical data from a situation similar to what is being modelled. It is often emphasized that empirical models give accurate predictions as long as they are utilized within the framework they were created (Mohren and Burkhart 1994). The descriptive nature of empirical models means that their ability to make predictions under changing conditions is limited (Bossel 1991). However, empirical models are very useful in formally describing and

quantifying relationships in a forest ecosystem on various temporal and spatial scales as long as there is a robust statistical relationship.

Process-based models attempt to quantify the mechanisms and processes which govern a forest ecosystem based on the current understanding of these processes. They often use a bottom-up approach where photosynthesis at the leaf level is the basis for tree and stand level growth (Zeide 2003). Traditionally process-based models have been used for understanding and explaining ecosystem structure and dynamics (Dixon *et al.* 1990), whereas applications in forest management are rare. This primarily owes to the poorer accuracy of process-based models (Mohren and Burkhardt 1994, Zeide 2003). The major advantage of this class of models is that they can cover changing conditions and higher complexity. Given that the basic relationships underlying a process-based model still hold it can be used for exploring and explaining forest dynamics rather than just describing it (Bossel 1991). To give accurate predictions models must be based on relationships that are well understood. It is often argued that since the understanding of forest ecosystems is becoming increasingly advanced, using process-based models in a forest management context for predictions is more relevant (Korzukhin *et al.* 1996, Messier *et al.* 2003).

An important point about empirical and process-based models is that there is a continuum between the two classes. According to Messier *et al.* (2003) process-based models normally use empirically derived relationships to some extent. A model will often rely on these relationships to make predictions about simple relations such as the diameter-height ratio for a single species. When modelling more complex interactions the understanding of different mechanism is relied upon.

Forest simulation models can be either stochastic or deterministic (Vanclay 1994). Given a set of conditions a deterministic model will give the same predictions for multiple simulations. A stochastic model tries to incorporate natural variability by introducing variation in modelling results. Especially in relation to applications in forest management this has a disadvantage: Since stochastic models do not give unambiguous answers (numeric models outputs are ranges rather than one result) it is more complicated to interpret model outputs. However, when simulating landscapes or complex forest ecosystems stochastic models may be more relevant because of the complexity of these systems. Given that outputs are a range of results it is possible to assess which risks are associated with different management scenarios.

Differentiation between spatially explicit and non-spatial models refers to the ability of a model to make predictions about multiple variables in a spatial context. Both stand and landscape level spatially explicit models have been developed. On a landscape level, the spatial distribution of different forest types (e.g. characterized by disturbance types, species and age-class composition) have a significant influence on ecological, economic and social response variables (Messier *et al.* 2003). On the stand level, complex stand dynamics are potentially better depicted through spatially explicit models (Porté and Bartelink 2002). Here the spatial distribution of individual trees is considered, especially in connection to both large and small scale disturbances.

The choice of modelling approach can be done according to the principle of “Occam’s razor”. It is the principle that an explanation of observations should be as simple as possible, but no simpler than necessary (Jeffreys and Berger 1991). If exclusively considering even-aged forest stands with very little spatial variation it is sufficient and efficient to use empirical stand level simulations model (*i.e.* non-spatial) for making long term predictions. When

modelling all-aged spatially complex stands it will most likely be necessary to use an empirical spatially explicit simulation model to achieve accurate predictions.

Modelling mortality in forest simulation models

Mortality is an important process in stand dynamics and forest succession (Kimmins 2004, Franklin *et al.* 1987). It is often characterized as a complex process which is difficult to quantify (Hawkes 2000). Furthermore it can arise from a range of biotic (e.g. between plant competition, disease, pests, browsing) and abiotic disturbance agents (e.g. fire, floods, landslides, avalanches, extreme weather, volcanic activities) (Oliver and Larson 1996). Mortality in forest tree populations occurring as a consequence of competition for above and below ground resources is often termed self-thinning (Yoda *et al.* 1963, Harper 1977, Peet and Christensen 1987) or density dependent mortality (Kimmins 2004). Light is in many cases the limiting resource (Kimmins 2004). Regular mortality (Vanclay 1994, Oliver and Larson 1996) covers density dependent mortality as well as mortality arising from stochastic events and more infrequent occurrences of pests, diseases and abiotic disturbances. A classic theory of the underlying process of density dependent mortality was proposed by Yoda *et al.* (1963). It states that at a given time a site will only be able to sustain a certain biomass. Mortality is a consequence of this limitation. The magnitude of the sustainable biomass is determined by the productivity of the site (length of the growing season, precipitation, nutrient availability etc.).

Vanclay (1994) distinguishes between theoretical and empirical approaches to modelling mortality. However, talking of purely theoretical approaches to modelling mortality is probably not appropriate as even theoretical approaches need to be validated through empirical data to be relevant in practice.

Theoretical approaches

According to Vanclay (1994) classic theoretical approaches to quantifying self-thinning include Reineke's stand density index (Reineke 1933) and the self-thinning line proposed by Yoda *et al.* (1963). Self-thinning generally applies to even-aged populations of a single species. These approaches assume that there is a fixed relationship between tree population density and maximum biomass capacity (*i.e.* mean tree size). The relationship is usually depicted through plotting mean tree size against density on logarithmic scales. The maximum size-density limit is represented by a line with a slope of approximately $-3/2$, termed the self-thinning line. The location of the self-thinning line is primarily related to species (Farnden 1996, Monserud *et al.* 2004), but variation between sites can also be considerable (Bi 2001). The self-thinning relationship (also known as the self-thinning rule) has been used frequently in predicting stand development, foremost in stand density management diagrams (e.g. Drew and Flewelling 1979, Farnden 1996). The major advantage of the self-thinning rule is that it provides an elegant and conceptually clear representation of the effects of competition for above and below ground resources on stand density. However, the generality of the self-thinning rule has often been questioned (White 1981, Westoby 1984, Zeide 1987, Norberg 1988, Lonsdale 1990, Reynolds and Ford 2005). It is impossible to derive a universal law that describes variation in a satisfactory manner. The self-thinning rule is often criticized for being

too simplistic to properly embrace the variation in self-thinning: The mean individual is not always a good measure of the population, total resources are not necessarily fully utilized during competition, often stands do not have a homogenous horizontal structure and different initial stand densities lead to different densities after density-dependent mortality (Reynolds and Ford 2005). The lack of adherence to details that describe and potentially influence the process of self-thinning also speaks against the self-thinning rule (Vanclay 1994, Reynolds and Ford 2005). Some efforts to modify the self-thinning rule have been made to improve its generality: E.g. by incorporation of site effects in a three dimensional self-thinning surface (Bi 2001).

According to Vanclay (1994) alternative theoretical approaches to modelling self-thinning on the stand level focus on height and crown competition rather than density. Underlying these alternative approaches is the basic concept that limited resources will regulate the tree population by a relationship between some tree attribute and mortality. Some examples of how mortality has been modelled are: (1) a measure of how many trees are overtopped in the population (Mitchell 1969, 1975), (2) a crown competition factor (Arney 1985), (3) a fixed relation between mean stand diameter increment and decrease in stand density (Leak 1969), (4) somewhat arbitrary rules of tree removal (e.g. every third tree under a certain size) (Campbell *et al.* 1979), (5) a rule of minimum allowable crown length relative to tree height (Arney 1972), (6) a threshold increment (Newnham 1964, Botkin *et al.* 1972, Reed 1980). Of the above mentioned, using a threshold increment has found most empirical support.

Empirical approaches

Empirical models of mortality build exclusively on relations derived from empirical data. Predicting probability of survival or mortality either for the average tree or for individual trees is a common approach. The goodness of fit of statistical relationships between mortality and various tree attributes is highly dependent on the available data. Still model developers usually confine themselves only to utilize relationships that are biologically believable (Fridman and Ståhl 2001, Yang *et al.* 2003).

Mortality models are often fitted with logistic regression as mortality is a yes(1) or no(0) outcome (Vanclay 1994). A further advantage of using the logistic regression is that it is suitable for using individual tree data. Thereby a high degree of detail is extracted from the data. Usually a regression function will express a probability of mortality for individual trees, which is either predicted directly or distributed to individual trees from stand/plot level mortality. Examples of the logistic regression function in mortality modelling are Monserud (1976), Monserud and Sterba (1999), Fridman and Ståhl (2001), Eid and Tuhus (2001), Justas *et al.* (2003) and Yang *et al.* (2003). According to Monserud and Sterba (1999) most cumulative distribution functions will work as the basic function for which parameters are estimated from empirical data. They mention the logistic or logit functions (very common), the Weibull, the gamma, the Richard's, the exponential, normal and the probit distribution functions as examples. Parameter estimation according to the least square, maximum likelihood or non-linear regressions methods is common (Monserud and Sterba 1999). Alternative empirical approaches to using regression models include functions derived from a combination of survival analysis and empirical data (Wyckoff and Clark 2000) as well as functions based on competition indexes (e.g. He and Duncan 2000, Zhao *et al.* 2006).

Empirical mortality models are often based on more than one predictor variable. Selection of appropriate predictor variables should not only be based on test statistics, but also on basic understanding of how forest ecosystems function and how factors contributing to mortality are expressed. Adherence to the modelling framework in which the mortality model will be used is also important. Some tree attributes are highly correlated, meaning that it is only necessary to include one in the mortality model to get good fit to data (Vanclay 1994). Hawkes (2000) classified predictor variables used in a wide range of mortality models. Classes which relate to density-dependent mortality are size, competition and carbon balance/growth. Tree size (e.g. diameter, height) is assumed to be related to the competitive status of the tree, especially when size relative to neighbouring trees is considered. Competition is usually expressed through canopy crowding or height/crown ratios. The basic assumption, that plants need to grow to survive motivate the use of growth variables. Growth integrates age, size, abiotic factors and competition as the carbon balance (expressed in growth) of a tree is affected by these factors. Diameter increment has often been used as a predictor of mortality (e.g. Monserud 1976, Buchman *et al.* 1983, Kobe *et al.* 1995, Kobe 1996, Kobe and Coates 1997, Wyckoff and Clark 2000, Bigler and Bugmann 2003, van Mantgem *et al.* 2003). Alternative growth variables include growth efficiency and ratios between biomass and growth (Hawkes 2000). Site variables have frequently been included in mortality models, but Vanclay (1994) states that the effect of site productivity on mortality is ambiguous: Density dependent mortality should express itself earlier on better sites giving higher mortality. On the other hand better sites have the capacity to support higher densities.

The mortality process is characterized by having some degree of stochasticity. Consequently many forest simulation models will contain a random mortality function on top of empirical mortality functions to account for tree death that is not related to the mechanisms captured in the model.

The basic process of mortality in complex stands is the same, but evidently interactions are more complex. Classic theoretical approaches often perform poorly in complex stands (Reynolds and Ford 2005). Logically individual tree approaches are more suited in complex stands. Stand averages in terms of mortality will be less useful because of the high degree of variability. Unless the same conditions apply in the stand being modelled as in the data used for parameterization, the model will most likely produce inaccurate predictions (Hawkes 2000). Competition for resources affects the individual tree similarly whether in even-aged single species stands or in complex stand, but must be quantified on the individual tree level to give meaningful predictions. Whether or not a model can handle complex stand to a large degree depends on whether the growth sub-models are able to reflect the competition and interactions between trees of different species and size, thereby providing useful individual tree attributes.

Modelling mortality in process-based forest simulation models

Forest simulation models are seldom based entirely on basic mechanisms of tree physiology such as photosynthesis. The major problem lies in scaling these mechanisms to the stand or forest levels (Dixon *et al.* 1990). In process-based models tree mortality typically follows a simple rule: It occurs when a tree stops growing (Hawkes 2000). Efforts to link processes of tree growth with stand and forest level dynamics have resulted in gap models such as the JABOWA-FORET family of models (Botkin *et al.* 1972, Botkin 1993, Shugart 1998). This group of models does not contain direct physiological models on a sub-tree level (e.g. branch, shoot, foliage), but link to the processes by having very specific growth functions considering resources and conditions such as light, temperature, water and nutrients on an individual tree level. Since there is a tight link between the growth mechanisms, carbon-balance of the individual tree and its predisposition to mortality, mortality functions rest on the growth model and the simple rule mentioned above. A probability of mortality is assigned to each tree and this is increased considerably as a tree becomes older and when it falls below a certain growth threshold (Hawkes 2000). Thus, even process-based models rely on the relationship between growth and mortality observed in empirical data (Clark 1992). The actual internal mechanisms of tree death are so poorly understood that to the knowledge of the author, it has not been attempted to create simulation models covering this.

SORTIE-ND

SORTIE is an individual tree, spatially explicit mixed species forest model, which makes predictions on the tree and stand levels (Pacala *et al.* 1993, Pacala *et al.* 1996, Messier *et al.* 2003, Coates *et al.* 2003, Astrup and Larson 2005). It was initiated and parameterized from field data, but builds on the understanding of processes simulated in many gap models. Consequently, SORTIE has an intermediate position between pure empirical and process-based models. Each tree within a modelled plot have (x, y) coordinates and a representation of the crown to account for both the horizontal and vertical structure of the stand. In the basic structure, SORTIE has five types of sub-models: (1) model of light availability, (2) growth models based on resource (light) availability, (3) seedling recruitment model, (4) sub-canopy growth model (juvenile and suppressed trees) and (5) tree mortality models. Finally SORTIE has a very flexible user interface making it applicable in a wide range of contexts.

The original version of SORTIE was developed and parameterized for studying succession in transitional oak – northern hardwood forests in the northeastern United States (Pacala *et al.* 1993, Pacala *et al.* 1996). It was a descendent of the JABOWA-FORET family of models (Botkin *et al.* 1972, Botkin 1993, Shugart 1998), which are a widely used group of gap dynamics models. Characteristic of these models is their use of light driven growth functions for trees with different vertical positions in a gap. The similarity between SORTIE and JABOWA-FORET models is the basic structure with growth, recruitment, mortality and resource sub-models. The main differences are: SORTIE requires parameterization from field measurements for all relations, the light sub-model is spatially explicit and growth in SORTIE is mediated by light availability, nutrient availability and crowding (below ground competition) (Astrup and Larson 2005).

SORTIE/BC was a further development of the original model. It was parameterized for mixed species stands in the interior cedar-hemlock forests of northwestern British Columbia as well as boreal mixedwoods (aspen-spruce forests) across Canada and southern temperate hardwood forest in Quebec. While retaining the basic structure of the original model SORTIE/BC was changed to allow for cuttings and planting to be carried out during simulations and to adapt it to the ecological conditions outside its original focus area (Coates *et al.* 2003). This was mainly done through parameterization from empirical data and the addition of alternative sub-models. SORTIE/BC thereby became more versatile and was better suited to deal with management issues (Astrup and Larson 2005).

SORTIE-ND (neighbourhood dynamics) is a restructured and re-written version of SORTIE and SORTIE/BC. A new feature in SORTIE-ND is a higher degree of flexibility in terms of which processes (termed behaviours) are set to act on a population of trees. All behaviours and related parameters are user-specified. It is possible to perform many different simulations and the model can be fitted to a wide range of specific conditions. Furthermore, the design of the SORTIE-ND code makes it simple to further develop the model.

Applications of the SORTIE models

Given the improved flexibility in SORTIE/BC and SORTIE-ND, they have been used for a range of different studies of forest dynamics in natural settings and in exploring implications of management. Table 1 summarizes how SORTIE/BC and SORTIE-ND have been applied in different studies around the World.

Table 1: Summary of studies utilizing SORTIE models.

| Region | Applications | References |
|--------------------------|--|---|
| Northeastern USA | <ul style="list-style-type: none"> • Forest succession and population dynamics. • Effects of variation in soil nutrients, herbivory and invasive species on forest succession. • Parameterization for exploring sustainable forest management strategies. | <p>Pacala <i>et al.</i> (1993, 1996), Canham <i>et al.</i> (2006), Papaik <i>et al.</i> (2006)</p> <p>Finzi and Canham (2000), Kobe <i>et al.</i> (2002), Catovsky <i>et al.</i> (2002), Schnurr <i>et al.</i> (2004), Papaik <i>et al.</i> (2005)</p> |
| British Columbia, Canada | <ul style="list-style-type: none"> • Stand dynamics and implications of partial harvesting in interior cedar-hemlock forests. • Stand dynamics, growth and yield and stand development after mountain pine beetle infestations in sub-boreal forests. • Implications of partial harvesting in boreal mixed-woods. • Productivity and stand development in southern interior montane forests. | <p>Coates <i>et al.</i> (2003), Lepage <i>et al.</i> (2000), Coates and Burton (1999), Canham <i>et al.</i> (2004), Canham <i>et al.</i> (1999), Wright <i>et al.</i> (1998)</p> <p>Astrup and Larson (2005), Coates <i>et al.</i> (in prep.)</p> <p>Coates <i>et al.</i> (2003)</p> <p>Simard <i>et al.</i> (in prep.)</p> |
| Quebec, Canada | <ul style="list-style-type: none"> • Effects of natural disturbances in hardwood forests. • Evaluation of management strategies using partial harvesting in temperate hardwood forests. Effects on stand dynamics and species diversity. • Interactions and effects of natural disturbances (fire and insects) on stand structure and composition in southern boreal mixed species forests. Regeneration and species diversity as an effect of spatial variation in seedling recruitment and understory cover of shade tolerant species. • Regeneration dynamics and implications of alternative harvesting approaches in boreal black spruce and boreal mixed-woods. Exploring the ecological and silvicultural implications of using natural regeneration. Linking to a landscape level model. | <p>Tremblay <i>et al.</i>(2005)</p> <p>Beaudet <i>et al.</i> (2002)</p> <p>Messier (in prep.)</p> <p>Messier (in prep.)</p> |
| Labrador, Canada | <ul style="list-style-type: none"> • Modelling stand dynamics. Linking to landscape level models. Evaluation of different stand management strategies. | (LFMI 2006) |
| Puerto Rico | <ul style="list-style-type: none"> • Mortality and regeneration dynamics after hurricane disturbances. • Long term dynamics of forest structure, composition and diversity in relation to hurricane frequency and severity. | <p>Uriarte <i>et al.</i> 2005</p> <p>(LFDP 2005)</p> |
| New Zealand | <ul style="list-style-type: none"> • Modelling influence of introduced mammals on regeneration and stand development in indigenous forests. • Links between browsing, tree species composition and decomposition/nutrient cycling. • Exploration of management scenarios. | <p>(Landcare Research 2006a)</p> <p>(Landcare Research 2006b)</p> |

Structure and flow of SORTIE-ND

SORTIE-ND was evaluated by Astrup and Larson (2005). In this study the logic and conceptual structure of the model was evaluated and the predictive abilities were tested for mixed species stands in the boreal and sub-boreal forests in northern British Columbia. A thorough description of model structure and sub-models is given in Astrup and Larson (2005). Figure 1 has been adopted from Astrup and Larson (2005) and shows the basic structure of SORTIE-ND configured for simulating both single species even-aged and complex stands in the present study.

The basic input of a model simulation is the diameter and spatial distribution of trees in the stand as well as a description of plot size and geographical location. Alternatively SORTIE-ND generates a random stem map from given density, species and size distributions. Tree allometry is estimated from empirically derived relations between DBH and height, crown depth and crown width.

The light behaviour is what drives SORTIE-ND simulations. The amount of light an individual tree receives is calculated from its crown dimensions, the dimensions and position of its neighbours and local light conditions.

Juvenile growth is a function of light and tree size (diameter at 10 cm). Adult growth is generated by the NCI-growth behaviour. This behaviour was developed and parameterized by Coates *et al.* (in prep.) and is a multiplicative version of the additive model presented by Canham *et al.* (2004). NCI refers to neighbourhood competition index. This index is calculated for each tree from the size and distance of neighbouring trees. The effects of target tree size (DBH), local environmental conditions and crowding from neighbouring trees are used to reduce an estimated maximum potential diameter growth (Canham *et al.* 2006):

$$\text{Growth} = \text{Max Growth} * \text{Size Effect} * \text{Shading Effect} * \text{Crowding Effect} * \text{Damage Effect}$$

The parameters that act to reduce the max growth parameter all have values between 0 and 1. The size effect is calculated from the DBH of the target tree as maximum growth is attained at a certain size (Canham *et al.* 2004). Shading effect is determined from the amount of shading cast from neighbouring trees and is calculated based on the light behaviour. The crowding effect is calculated directly from the NCI value.

Three mortality behaviours for both juvenile and adult trees were applied in the study by Astrup and Larson (2005). Juvenile and adult random mortality is an assigned annual species specific probability of mortality (0.25–1.00%). As it is difficult to estimate random mortality rates from field data, they were set according to previous experience with adjusting model performance to give realistic predictions (Astrup pers. comm.). Competition mortality is mortality related to low growth for adult trees, while BC mortality is the same for juvenile trees. The predictor variable in both these mortality functions is annual radial increment predicted by the growth behaviours mentioned above. Density self-thinning is only applied to juvenile aspen and simulates thinning processes in root suckers. Senescence mortality is mortality due to old age (large DBH).

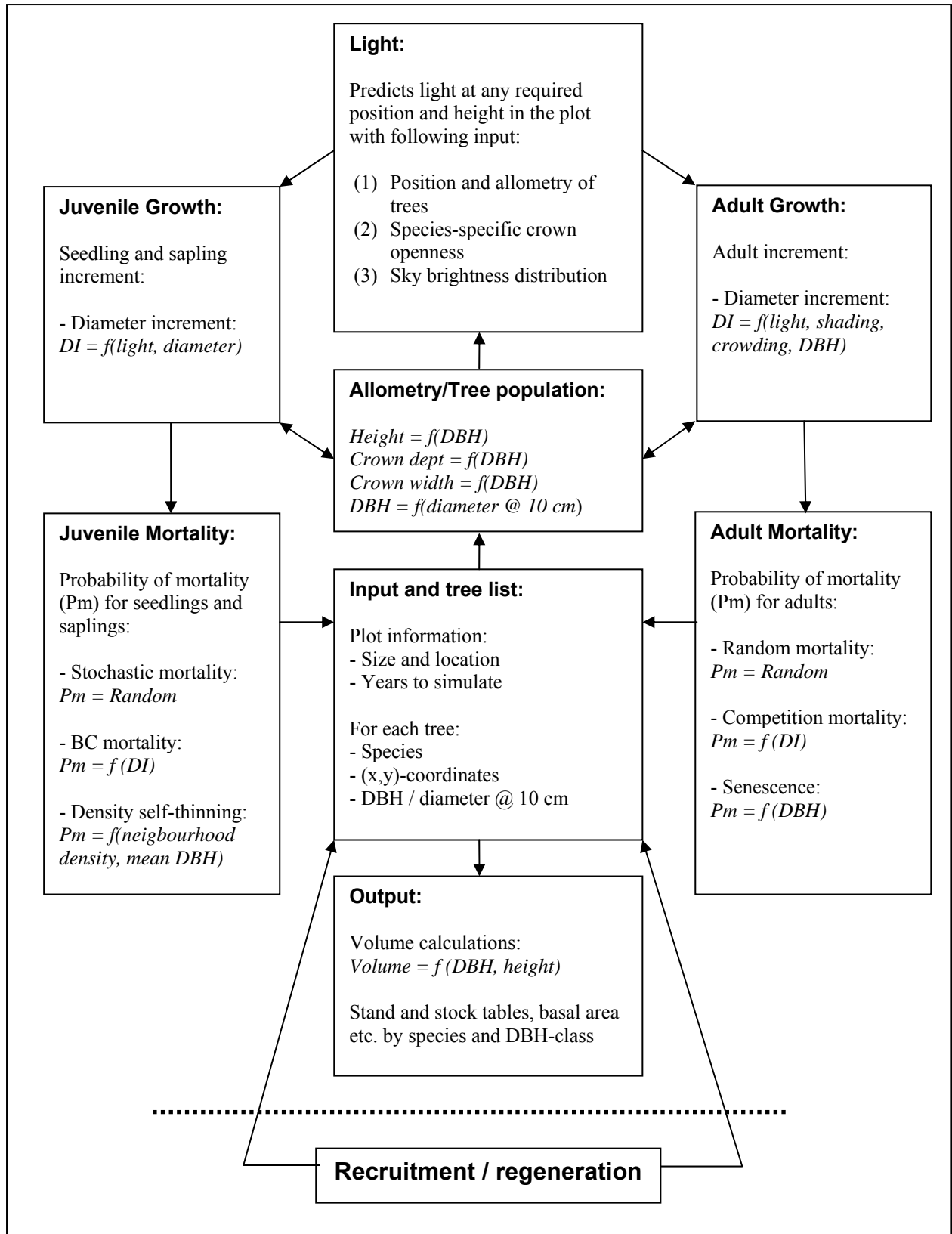


Figure 1: Basic structure and model flow of SORTIE-ND as configured by Astrup and Larson (2005) for simulations of boreal and sub-boreal mixed species stands. The recruitment behaviour inserted under the dashed line was not included.

It is possible to assign other growth and mortality behaviours depending on the conditions that are being simulated. E.g. the effect of nutrient availability can be included in the growth behaviour and herbivory can occur as a mortality behaviour for juvenile trees. Furthermore a recruitment/regeneration behaviour is normally included when simulating the effects of natural disturbances or silvicultural interventions (Coates *et al.* 2003). Finally it is also possible to simulate snags.

The model output consists of tree and stand level measures of density, basal area and volume. This can be presented both according to species and DBH-classes.

SORTIE-ND is shareware and available through the internet (www.sortie-nd.org). It has an open source code, but it is the ambition of the original model developers to coordinate the incorporation of any improvements and continuously update SORTIE-ND in shareware versions. The SORTIE models have shown to be very useful tools for exploring stand dynamics in complex stands in connection to stand dynamics research. However, also management issues have been addressed through SORTIE and it is reasonable to expect more emphasis on SORTIE as a management tools in the future. Implementation of e.g. ecosystem management, calls for improved support tools that can deal with ecological, social and economic aspects of management of complex stands. Further improvements of the basic sub-models are imperative for making reliable and accurate predictions with SORTIE-ND. This was firmly verified in the model evaluation conducted by Astrup and Larson (2005). In this study it was found that improved growth and mortality sub-models would improve the predictive abilities of the model.

Problem statement

Tree mortality is an important process in forest ecosystems. To make accurate predictions, forest simulation models rely on mortality sub-models. A range of approaches to modelling mortality exist. Empirical approaches have been widely used with satisfactory results. In the specific case of the individual tree, spatially explicit mixed species forest model SORTIE-ND, an empirical model for adult tree mortality would potentially improve the predictive abilities of the model. In this model framework a growth based mortality model is most convenient because of the basic model structure and outputs. SORTIE-ND has been used extensively in British Columbia for research purposes.

The main problem in empirical approaches to modelling mortality is to provide sufficient data, especially when predicting mortality from tree growth. Ideally permanent sample plot data can be used, but such long term data is rare. This makes it relevant to use alternative approaches to obtain growth data from individual trees. The basic method used by Kobe *et al.* (1995), Kobe (1996), Kobe and Coates (1997) and Kneeshaw *et al.* (2006) parameterizes growth based mortality functions from tree ring data collected from live and dead saplings. It provides a straight forward approach to deriving empirical mortality functions from field data and has been used successfully for juvenile trees. However, it has never been applied to adult trees.

The primary objective of this study is to test the empirical approach for parameterization of growth based individual tree mortality models previously used for juvenile trees. It will be tested on adult trees of four common tree species in the sub-boreal forests of British Columbia. Secondly the study aims at evaluating how the new empirical mortality models for adult trees perform. This will be done by incorporating them into SORTIE-ND and performing simulations of single and mixed species stands.

Methods

Basic modelling approach

When dealing with complex stands the most appropriate approach to modelling mortality would probably be to predict mortality from the actual competition that the individual tree is exposed to at a given time (Zhao *et al.* 2006). To parameterize mortality models based on actual competition a very large amount of detailed data from stem mapped plots would be needed (Astrup pers. comm.). Specifically, the exact position of each tree and its neighbours would be needed along with detailed individual tree data. This would require an inappropriately large sampling effort.

Basing mortality models on the assumption that factors which affect tree vigour are expressed in growth rate makes for a more straight-forward approach. Using growth rate as the predictor according to the method of Kobe *et al.* (1995), Kobe (1996), Kobe & Coates (1997) and Kneeshaw *et al.* (2006) requires a relatively small sampling effort. In SORTIE-ND, the competition that the individual tree is exposed to is expressed in the neighbourhood competition index (NCI). Radial growth of the individual tree is a direct function of this index as well as shading from neighbouring trees. Consequently, using growth as a predictor of mortality in the SORTIE-ND framework also indirectly incorporates actual competition in the mortality model, giving this approach further support.

Study area and species

The study area is located near Smithers in northwestern British Columbia (54°45'N, 126°15'W) (Figure 2). All of the sixteen study sites are in the Sub-Boreal Spruce Zone (SBS) and either in the Moist Cold Subzone Babine Variant (SBSmc2) or the Dry Cool Subzone (SBSdk) (Table 2). In the study area the SBSmc2 occurs at middle elevations and the SBSdk at lower elevations (valley bottoms). These subzones are classified according to the Biogeoclimatic Ecosystem Classification System (BEC) (Krajina 1969) and are described in detail by Banner *et al.* (1993). Mixtures of few coniferous species dominate stands in both subzones, but deciduous species can also be significant components. The study focused on the four most common tree species in the subzones: trembling aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*), hybrid spruce (a complex of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

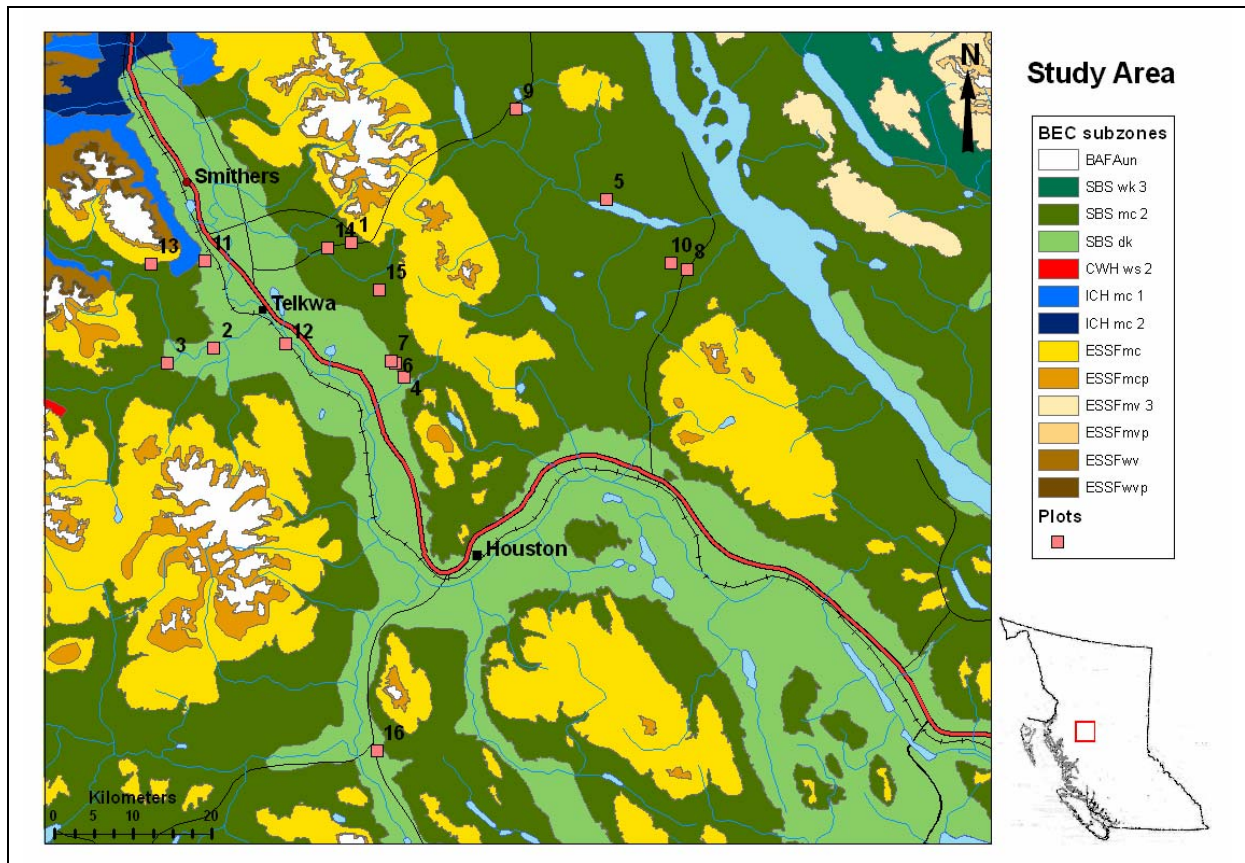


Figure 2: Map of the study area with study sites. Vegetation zones are classified according to the Biogeoclimatic Ecosystem Classification System (BEC) (Krajina 1969): BAFA = *Boreal Altai Fescue Alpine*; SBS = *Sub-boreal Spruce*; CWH = *Coastal Western Hemlock*; ICH = *Interior Cedar Hemlock*; ESSF = *Engelmann Spruce Sub-alpine Fir*.

Field sampling and growth measurements

A field sampling method similar to Kobe *et al.* (1995), Kobe & Coates (1997) and Kneeshaw *et al.* (2006) was used. However, as adult trees and older stands were sampled the approach was slightly modified. The objective of the sampling was to obtain a dataset containing overall mortality rates and measurements of density, tree size and recent radial growth for both live and recently dead trees. In this study recently dead trees are defined as trees that died within a 5 year period before sampling.

Mature stands in the study area generally have relatively low densities and mortality rates. Thus, it was difficult to obtain large samples of a single species from a single site. For each species, we sampled several sites (3-6) and pooled these as one sample to obtain a total sample size of approximately 70 recently dead and live trees for each species. A total of sixteen sites were sampled of which two were sampled for two species. Sampling sites were selected so each site should give an appropriate sample size (>5 recently dead trees) and have variation in both recent radial growth rates and tree size. Predominately, dense stands in the stem exclusion stage were sampled as they have high competition for above and below ground resources, gave an adequate sample in a reasonably small area and have both dominant, co-dominant, and suppressed trees. Mortality in these sites was foremost to arise

from competition and any stands with obvious significant mortality arising from pathogens or insects were avoided.

The individual sites were square and to avoid edge effects plot boundaries were no closer than 10 m from any forest edge. The sampling sites ranged in area from 745 to 22,000 m² and contained 4 to 50 recently dead and live trees (Table 2). Two sites (site 6 and 9) had sufficient recently dead trees to be sampled for two species. At each site each focal species (one or two) was considered separately. The total number of live trees in a site was estimated by sub-sampling of 4-10 circular (radius 6 or 8 m) random plots depending on the size of the sampling site. The total sub-plot area for each sampling site can be found in Table 2. The number of recently dead trees was determined by a census of the site.

For each site all recently dead trees and an equal number of live trees of the focal species were randomly sampled. For each sampled tree an increment core was taken at breast height and diameter at breast height (DBH) was measured. Only trees with DBH > 5cm and trees that had no signs of pathogens or insects were sampled. The increment cores were measured with a 40X stereo microscope and a Parker Instruments digital readout (resolution: 0.01 mm) connected to a PC with the Nutricom AGRMM Ring Width Analyzer Program (version 1.1, REA Engineering Services, 1988). The 20 most recent growth rings in each core were measured. A total effective sample size of recently dead trees of 86, 120, 70 and 69 was achieved for aspen, lodgepole pine, hybrid spruce and subalpine fir respectively (Table 2). Due to damaged cores the number of usable samples is slightly lower than the number which was actually sampled (Table 2).

After a certain period of time dead trees will decay to an extent where estimation of time since death becomes increasingly difficult. For the species studied by Kobe & Coates (1997), Bartemucci & Coates (unpublished manuscript) examined the physical changes of saplings after they had died as a result of manual brushing, thinning or spraying. They found that after three years it became increasingly difficult to determine the time since death from properties such as foliage, bud and fine branch retention and bark intactness. Kneeshaw *et al.* (2006) studied the change of sapling characteristics after death for eastern species and also used three years to discriminate between recently dead and older. For adult trees examining properties such as bud and fine branch retention to the extent that Bartemucci & Coates (unpublished manuscript) and Kneeshaw *et al.* (2006) did is difficult. We set a number of criteria for recently dead trees to support a subjective field assessment of whether individual trees of the focal species had died within 5 years. These criteria were derived from Bartemucci and Coates (unpublished manuscript):

- To be considered recently dead the bark had to be intact.
- Preferably dead trees were to have retention of dead foliage. If there was no retention the crown had to be intact (still having fine branching).
- The stem wood could not appear grey and outer portion of the xylem should preferentially contain resin.

Table 2: Description of sampling sites.

| Site No. | Name | Coordinates | Subzone | Site series | # samples ¹ live / dead | Area (m ²) | Sub-plot area ² (m ²) | Live # / ha | Dead # / ha | Annual mortality rate ³ (%) | Mean DBH ⁴ (cm) |
|--|-------------------------|-------------------------------|---------|-------------|---------------------------------------|------------------------|--|-------------|-------------|--|----------------------------|
| Trembling Aspen (<i>Populus tremuloides</i>) | | | | | | | | | | | |
| 2 | Telkwa River Rd. | N 54 39.078' W 127 10.376' | SBSdk | 01 | 12 / 14 (14 / 14) | 22000 | 2011 | 776 | 6 | 0.15% | 24.8 |
| 3 | Telkwa River Rd. | N 54 38.184' W 127 15.674' | SBSdk | 01 | 9 / 9 (9 / 9) | 1000 | 565 | 1804 | 88 | 0.95% | 15.8 |
| 5 | Fulton Lake Rd. | N 54 51.265' W 126 28.100' | SBSmc2 | 01 | 2 / 5 (5 / 5) | 2000 | 679 | 3566 | 22 | 0.12% | 8.3 |
| 11 | Hudson Bay Mountain Rd. | N 54 44.948' W 127 10.369' | SBSdk | 06 | 13 / 15 (15 / 15) | 8000 | 905 | 1404 | 19 | 0.27% | 17.2 |
| 12 | Lawson Rd. | N 54 39.815' W 127 01.522' | SBSdk | 01 | 17 / 15 (19 / 19) | 6000 | 905 | 1448 | 32 | 0.44% | 15.7 |
| 14 | Babine Lake Rd. | N 54 46.175' W 126 55.384' | SBSmc2 | 06 | 28 / 28 (29 / 29) | 5000 | 792 | 1768 | 58 | 0.64% | 17.4 |
| Lodgepole pine (<i>Pinus contorta</i>) | | | | | | | | | | | |
| 1 | Babine Lake Rd. | N 54 46.308' W 126 51.050' | SBSmc2 | 01 | 49 / 50 (50 / 50) | 5000 | 1018 | 2682 | 100 | 0.73% | 14.5 |
| 8 | Granisle Highway | N 54 44.206' W 126 12.359' | SBSmc2 | 01 | 32 / 33 (34 / 34) | 4000 | 679 | 2520 | 85 | 0.66% | 14.6 |
| 9 | Granisle Connector | N 54 55.512' W 126 33.633' | SBSmc2 | 01 | 9 / 9 (9 / 9) | 6000 | 792 | 386 | 15 | 0.76% | 23.3 |
| 10 | Paul Lake | N 54 44.960' W 126 15.395' | SBSmc2 | 01 | 28 / 28 (28 / 28) | 1000 | 679 | 3095 | 376 | 2.27% | 12.9 |
| Hybrid spruce (<i>Picea glauca x Picea engelmannii</i>) | | | | | | | | | | | |
| 4 | Canyon Creek Rd. | N 54 38.611' W 126 43.912' | SBSmc2 | 01 | 34 / 35 (35 / 35) | 10000 | 1131 | 2617 | 35 | 0.27% | 15.8 |
| 6 | Canyon Creek Rd. | N 54 39.270' W 126 44.797' | SBSmc2 | 01 | 17 / 16 (18 / 18) | 15000 | 1131 | 433 | 12 | 0.55% | 19.8 |
| 9 | Granisle Connector | N 54 55.512' W 126 33.633' | SBSmc2 | 01 | 6 / 6 (6 / 6) | 6000 | 792 | 599 | 10 | 0.33% | 20.0 |
| 15 | Canyon Creek Rd. | N 54 44.323' W 126 48.216' | SBSmc2 | 01 | 7 / 8 (8 / 8) | 3000 | 452 | 2100 | 26 | 0.25% | 14.9 |
| 16 | Morice-Owen FSR | N 54 11.734' W 126 50.965' | SBSdk | 01-06 | 4 / 4 (4 / 4) | 5000 | 679 | 1930 | 8 | 0.08% | 9.6 |
| Subalpine fir (<i>Abies lasiocarpa</i>) | | | | | | | | | | | |
| 6 | Canyon Creek Rd. | N 54 39.270' W 126 44.797' | SBSmc2 | 01 | 28 / 28 (28 / 28) | 15000 | 1131 | 1388 | 19 | 0.27% | 16.4 |
| 7 | Canyon Creek Rd. | N 54 39.494' W 126 45.075' | SBSmc2 | 01 | 28 / 28 (28 / 28) | 7000 | 905 | 2564 | 41 | 0.32% | 14.1 |
| 13 | McDonnell Lake FSR | N 54 44.626' W 127 17.193' | SBSmc2 | 01 | 14 / 14 (14 / 14) | 2000 | 452 | 2255 | 70 | 0.61% | 13.0 |

¹Numbers in brackets are sampled recently dead and live trees. Some cores had to be discarded giving fewer growth measurements (summed above the brackets).

²Total area of sub-plots. 4-10 circular sub-plots were used for determining density of live trees at each sampling site.

³ Annual mortality rate = $\left(\frac{\ln(\#live) - \ln(\#live+\#dead)}{\text{recently dead period}} \right) \cdot 100\%$

⁴ Estimated mean DBH for live trees at each site.

Model development

Ideally the mortality models should be parsimonious and have biologically interpretable parameters. In this context parsimony refers to a model form that is relatively simple, accurate and balanced in terms of bias and variance. With increasing model complexity (number of parameters) bias decreases and variance increases (Burnham and Anderson 2002). In comparable studies of sapling mortality (Kobe *et al.* 1995; Kobe 1996; Kobe and Coates 1997; Kneeshaw *et al.* 2006) several functional forms were tested. A two-parameter negative exponential decay function was found to fit mortality patterns of saplings well (Kobe *et al.* 1995; Kobe 1996; Kobe and Coates 1997). Additionally it has parameters that are easy to interpret:

$$\text{[Equation I]} \quad m(g) = P_0 \times e^{-r \times g}$$

g is the average annual radial growth over a given period, $m(g)$ is the annual probability of mortality, P_0 is the probability of mortality at zero growth, and r is the decay rate of the function (the sensitivity of the tree species to changes in radial growth and thereby to competition for above and below ground resources). If $g = 0$ the individual tree is experiencing high competition for above and below ground resources and P_0 can be expected to be close to 1 (Kobe and Coates 1997). When r is low $m(g)$ decreases slowly with increasing g and species with a relatively low r experience a higher probability of mortality and are more sensitive to competition. In relation to shade tolerance this implies that shade intolerant species like aspen and lodgepole pine are expected to have a lower r than more shade tolerant species like hybrid spruce and subalpine fir. Kobe *et al.* (1995) and Kobe (1996) used Equation 1 for saplings in the eastern hardwoods. Kobe and Coates (1997) derived a model form that incorporates flexibility both in the length of the recently dead period and the period to which probability of mortality applies. This model was further developed by Kneeshaw *et al.* (2006):

$$\text{[Model I]} \quad m(g) = P\{X \leq t\} = 1 - \exp(-t \times A \times e^{-B \times g})$$

$m(g)$ is the probability that a tree will die in the period t (not necessarily equal to the length of the recently dead period), g is a measure of radial growth, B is the decay rate of the model (same interpretation as r), A is a parameter relating to the probability of mortality at zero growth. $m(g)$ will approach a value between 0 and 1 dictated by A and t . This is the case because $e^{-B \times g} \rightarrow 1$ when $g \rightarrow 0$.

In this study, Model I was used as the most flexible model and is referred to as the Full model. Nested in Model I are two models. By setting $A = 1$ the Full model is reduced to:

$$\text{[Model II]} \quad m(g) = P\{X \leq t\} = 1 - \exp(-t \times e^{-B \times g})$$

This is also an exponential decay function and it is the basic model used by Kobe and Coates (1997). A null model can be derived from Model I by setting $B = 0$:

$$\text{[Model III]} \quad m(g) = P\{X \leq t\} = 1 - \exp(-t \times A)$$

This model yields an average probability of mortality and by testing it against the two other models it can be determined whether the chosen variable g is appropriate for predicting probability of mortality.

Predictor variable selection (Incorporating tree size into the model)

In this study, we tested absolute radial growth and radial growth relative to tree size as predictors of mortality. As tree size increase, the respiratory requirements increase leading to a stagnating or decreasing amount of photosynthates available for radial growth (Waring 1987, Givnish 1988). Furthermore, the biomass allocated to radial growth has to be distributed over a larger surface. With age this leads to decreasing width of growth rings even for trees experiencing virtually no competition for above and below ground resources. Consequently, for adult trees radial growth relative to tree size is potentially a better expression of tree vigour than absolute diameter growth.

An obvious measure of relative radial growth is absolute radial growth relative to DBH. However, radial growth is not likely to be directly proportional to diameter and relative basal area increment suffers from the same problem. A more informative measure of relative radial growth is absolute radial growth relative to potential radial growth. Potential radial growth is that of a ‘‘free growing’’ tree, *i.e.* a tree not limited by competition for above and below ground resources. Canham *et al.* (2004) approximated the potential diameter growth (*PotDG*) of a hypothetical free growing tree with a lognormal function:

$$\text{[Equation II]} \quad \text{PotDG} = \text{MaxDG} \times \exp \left[-\frac{1}{2} \times \left(\frac{\ln(\text{DBH} / X_0)}{X_b} \right)^2 \right]$$

Where *MaxDG* (mm/year) is maximum potential diameter growth, X_0 is the DBH (cm) where *MaxDG* occurs and X_b determines the breadth of the function. The equation is part of the NCI growth behaviour in SORTIE-ND where diameter growth is approximated by reducing *PotDG* according to light availability and crowding competition. Parameters (*MaxDG*, X_0 and X_b) for the four focal species in this study were estimated from a large dataset collected in the SBSmc2 subzone by Coates *et al.* (in prep.). Thus, relative radial growth (*RG*) is a non-linear transformation of absolute radial growth (*AG*):

$$\text{[Equation III]} \quad \text{RG} = f(\text{AG}, \text{DBH}) = \frac{\text{AG}}{(\text{PotDG}/2)}, \text{ where } 0 < \text{RG} < 1$$

Model selection

A total of six candidate models were tested for each species. The six models were constructed by combining the three functional forms (Model I - III) and two predictor variables (absolute and relative radial growth). For model selection we used likelihood ratio tests (LRT) and a second order variant of the Akaike Information Criterion (AIC_c).

A LRT is only appropriate when comparing nested models, meaning that one model can be derived from the other by assigning one or more parameters with the value 1 or 0. In this case Models II and III can be derived from Model I by setting $A = 1$ or $B = 0$. They are both nested in the Full model, but not in each other. A comparison of Model II and III was consequently not performed with a LRT.

AIC_c can be used when comparing both nested and non-nested models. It is an information theory model selection criterion developed by Hurvich and Tsai (1989). The AIC_c is based on the log-likelihood of the individual model, but assigns a penalty according to the number of parameters. Thus, model selection according to AIC_c ensures that the most parsimonious model is chosen. AIC_c is calculated according to:

$$\text{[Equation V]} \quad AIC_c = -2\log(\ell(\hat{\theta})) + 2K + \frac{2K(K+1)}{n-K-1}$$

$\ell(\hat{\theta})$ is the likelihood of the candidate model, $\hat{\theta}$ are the model parameter estimates, n the sample size and K the number of parameters. The best candidate model will have the lowest AIC_c and thereby a $\Delta AIC_c = 0$. If ΔAIC_c is 0-2 there is equal support for two models under consideration. If ΔAIC_c is 4-7 there is little support and if $\Delta AIC_c > 10$ the model fails in explaining a substantial amount of the variation exhibited in the data (Burnham and Anderson 2002).

Parameter estimation

The maximum likelihood method developed by Kobe *et al.* (1995) was used for parameter estimation. The original statistical software written by Kobe *et al.* (1995) and Kobe & Coates (1997) was further developed by Kneeshaw *et al.* (2006) under the name Quebec Mortality Estimator.

The maximum likelihood function in the Quebec Mortality Estimator was described by Kobe *et al.* (1995) as:

„(the likelihood of obtaining the data set) = (the probability of encountering D dead saplings and $N-D$ live saplings without respect to order) \times (the product of the probability densities that a dead individual had growth history g_i prior to its death) \times (the product of the probability densities that a live individual had growth history g_i).” (Kobe *et al.* 1995), p. 520)

Thus the likelihood function has three components. The first is the probability of having D dead trees and $N - D$ live trees without respect to order in a sample. According to Feller (1970) such a probability can be perceived as a series of Bernoulli trials since:

- There are two possible outcomes (dead or live) for each tree in a sample.
- The expected probabilities of a tree in the sample being dead (\bar{U}) or live ($1-\bar{U}$) are fixed.
- Whether the next tree in the sample is alive or dead is independent from previously examined trees.

The distribution of live and dead trees follows a binomial distribution:

$$[\text{Component I}] \quad \binom{N}{D} \times (\bar{U})^D \times (1-\bar{U})^{N-D}$$

where \bar{U} is calculated from the probability density function of growth rates $h(g)$ and the mortality model $m(g)$:

$$[\text{Equation VI}] \quad \bar{U} = \int_0^{\infty} m(g)h(g)dg$$

$m(g)$ is one of the mortality models (Model I-III) and $h(g)$ is specified as a gamma density function:

$$[\text{Equation VII}] \quad h(g) = \frac{\left(\frac{\alpha}{\beta}\right)^{\alpha} g^{\alpha-1} e^{-\alpha/\beta g}}{\Gamma(\alpha)}$$

The gamma density function was chosen because of its flexibility. The second component of the maximum likelihood function is the probability density function of growth rates prior to death for recently dead trees. This is based on the probability density function of growth rates for all trees $h(g)$ and the mortality function $m(g)$:

$$[\text{Component II}] \quad Y_D(g|dead) = \frac{h(g)m(g)}{\int_0^{\infty} m(g)h(g)dg}$$

The third component of the maximum likelihood function is the probability density function of prior growth rates of live trees. This function is analogous to the second component of the function:

$$[\text{Component III}] \quad Y_L(g|live) = \frac{h(g)[1-m(g)]}{1-\int_0^{\infty} m(g)h(g)dg}$$

In conclusion, the maximum likelihood function is:

$$[\text{Equation VIII}] \quad \ell(A, B, \alpha, \beta) = \binom{N}{D} (\bar{U})^D (1-\bar{U})^{N-D} \times \prod_{i=1}^{no.dead} \frac{h(g_i)m(g_i)}{\bar{U}} \times \prod_{i=1}^{no.live} \frac{h(g_i)[1-m(g_i)]}{1-\bar{U}}$$

Where *no. dead* and *no. live* are the number of sampled live and dead trees of a given tree species in all sampling site. N is the estimated total number of live trees of a given species in all sampling sites. D is the counted number of dead trees of a given species in all sampling sites. g_i is the radial growth (absolute or relative) of the individual sampled tree. We used the

average of the latest five complete years of growth, *i.e.* the year of measurement was not included. The Quebec Mortality Estimator uses a Metropolis algorithm (Metropolis *et al.* 1953; Szymura and Barton 1986) to search for the combination of parameters (A, B, α, β) in $h(g)$ and $m(g)$ that maximizes the likelihood function for a given mortality model (Model I-III). Further it gives confidence bounds (95% support intervals) for all parameter estimates which are produced through the inverted likelihood ratio test (Edwards 1992).

Results

Presentation of basic data

The basic data from the sampled plots was collected from stands with some variation in stand density and mean tree size (Table 2). Even though target stands were in the self-thinning phase there was substantial variation in stand densities and mean tree size. Density dependent mortality was obvious in all stands given the number of recently dead trees (Table 2). Relative radial and absolute growth rates plotted against DBH for recently dead and live trees are depicted in Figures 3a and 3b respectively. Across all species the transformation from absolute to relative growth rates does not alter the general distribution of the data.

Generally variation in radial growth for live trees is large. However there seems to be a trend for increasing growth with tree size for aspen, lodgepole pine and subalpine fir. For hybrid spruce this trend is less clear. Large dominant trees in self-thinning stands will tend to have better vigour and grow faster. Consequently variation in relative radial growth for recently dead trees is smaller. For all species most recently dead trees grew in the relative radial growth interval of 0.01-0.03 prior to their death. There is also a concentration of smaller live trees in this growth interval.

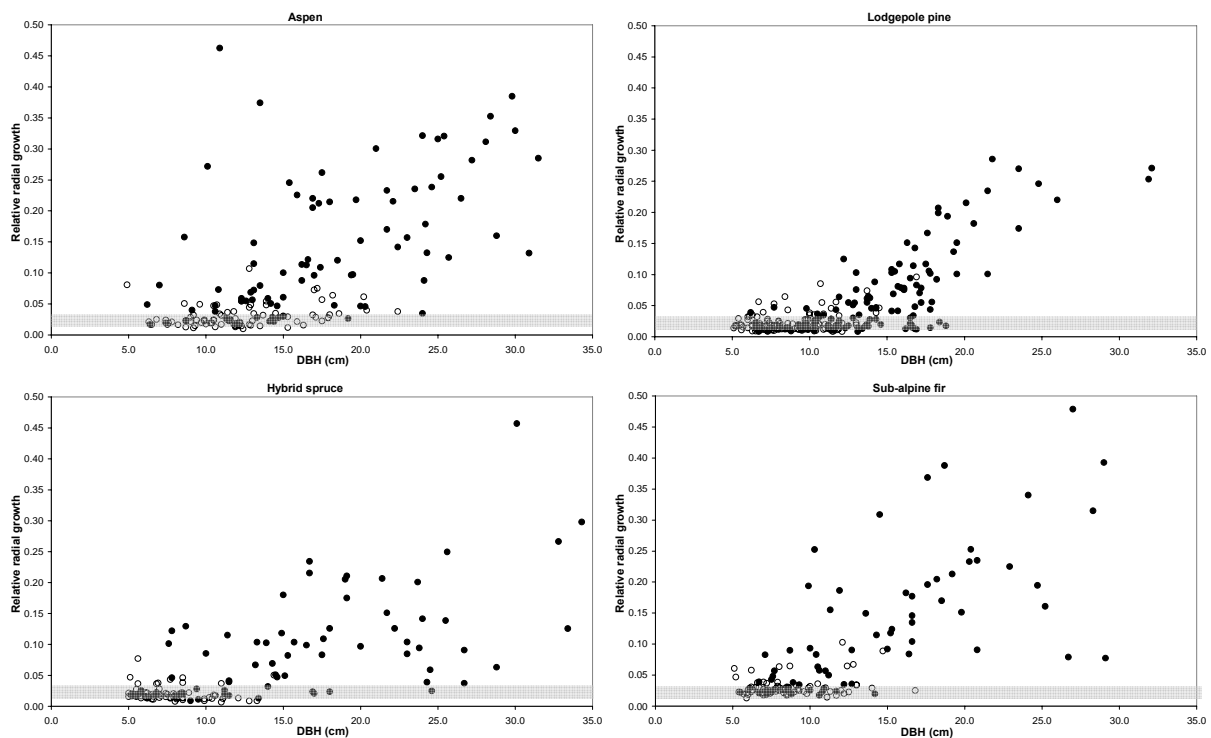


Figure 3a: Scatterplots of the basic data for the four focal species. Average (of 5 years) annual relative radial growth plotted against DBH for live (●) and recently dead (○) trees. The shaded area is the relative radial growth interval 0.01-0.03.

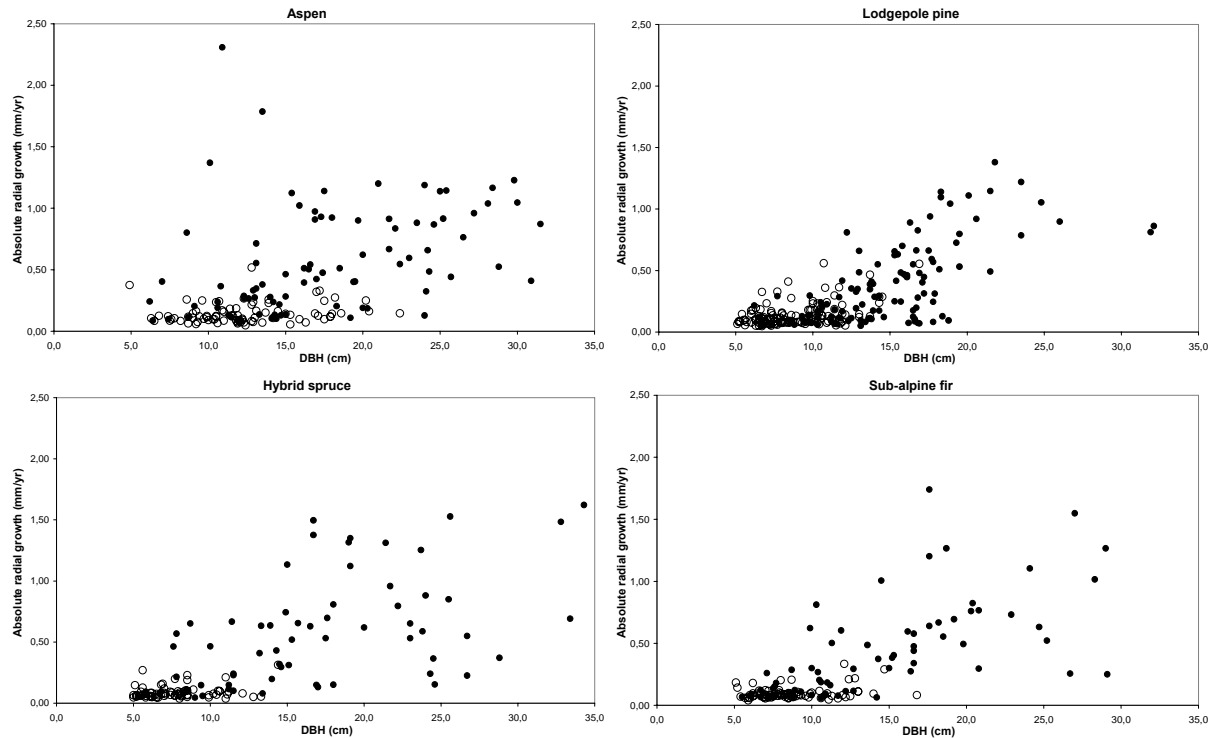


Figure 3b: Scatterplots of the basic data for the four focal species. Five year average annual absolute radial growth plotted against DBH for live (●) and recently dead (○) trees.

Model selection

Generally, the LRTs and AIC_c indicated that for all species the Full model (Model I) is the best approximating model. The only exception is for aspen and lodgepole pine with absolute radial growth. For all species the reduced model (Model II) has a $\Delta AIC_c > 10$ (Table 3) irrespective of which predictor variable is used.

Predictor variable selection

Relative radial growth was found to be the best predictor variable (Table 3). Of the three models, AIC_c ranks Model I highest across all species when using relative radial growth. LRTs also support that Model I generally fit the data better than Model II and III. This implies that relative radial growth is a better predictor of mortality than absolute radial growth irrespective of the species under consideration.

With absolute radial growth as predictor variable, the best aspen and lodgepole pine model is the null model (Model III). Thus, for these species absolute radial growth is not a good predictor of mortality and assigning a fixed probability of mortality to all trees gives better fit to the data. The LRTs for these two species also supported this finding. For hybrid spruce and subalpine fir both AIC_c and LRTs show that using absolute radial growth in the Full model (Model I) gives a better fit than the null model (Model III).

Table 3: Negative log-likelihoods, ΔAIC_c , and LRT statistics for the three different model formulations denoted in the text as Model I, II and III¹. Models using absolute radial growth (AG) in (a) and relative radial Growth (RG) in (b).

| Species | Model ¹ | Variable ² | $-\ln(\ell)$ | ΔAIC_c | Rank | LRT ($\chi^2_{(\alpha=0.05, df=1)} = 3.84$) |
|----------------|--------------------|-----------------------|--------------|----------------|------|--|
| (a) | | | | | | |
| Aspen | I | AG | -391.6 | 90.7 | 3 | 0.0 |
| Aspen | II | AG | -367.8 | 40.9 | 2 | 426.0 |
| Aspen | III | AG | -347.3 | 0 | 1 | -169.9 |
| Lodgepole pine | I | AG | -389.7 | 172.0 | 3 | 0.0 |
| Lodgepole pine | II | AG | -602.7 | 595.9 | 2 | -47.6 |
| Lodgepole pine | III | AG | -304.8 | 0 | 1 | -88.6 |
| Hybrid spruce | I | AG | -251.4 | 0 | 1 | 0.0 |
| Hybrid spruce | II | AG | -266.5 | 28.2 | 2 | 30.3 |
| Hybrid spruce | III | AG | -283.4 | 62.0 | 3 | 64.1 |
| Subalpine fir | I | AG | -222.7 | 0 | 1 | 0.0 |
| Subalpine fir | II | AG | -241.3 | 35.0 | 2 | 37.1 |
| Subalpine fir | III | AG | -247.4 | 47.3 | 3 | 49.4 |
| (b) | | | | | | |
| Aspen | I | RG | 62.4 | 0 | 1 | 0.0 |
| Aspen | II | RG | 43.2 | 36.3 | 2 | 38.4 |
| Aspen | III | RG | -158.1 | 438.9 | 3 | 441.0 |
| Lodgepole pine | I | RG | 101.6 | 0 | 1 | 0.0 |
| Lodgepole pine | II | RG | 20.4 | 160.3 | 3 | 162.4 |
| Lodgepole pine | III | RG | 58.3 | 84.6 | 2 | 86.6 |
| Hybrid spruce | I | RG | 157.9 | 0 | 1 | 0.0 |
| Hybrid spruce | II | RG | 145.3 | 23.1 | 2 | 25.3 |
| Hybrid spruce | III | RG | -58.4 | 430.5 | 3 | 432.6 |
| Subalpine fir | I | RG | 91.5 | 0 | 1 | 0.0 |
| Subalpine fir | II | RG | 71.5 | 37.9 | 2 | 40.0 |
| Subalpine fir | III | RG | -88.3 | 357.4 | 3 | 359.5 |

¹Model I: $m(g) = P\{X \leq t\} = 1 - \exp(-t \times A \times e^{-B \cdot g})$; Model II: $m(g) = P\{X \leq t\} = 1 - \exp(-t \times e^{-B \cdot g})$;

Model III: $m(g) = P\{X \leq t\} = 1 - \exp(-t \times A)$

²AG: Absolute radial growth (mm/yr); RG: Relative radial growth (0 < RG < 1)

Parameter estimates and model illustrations

The maximum likelihood estimates of parameters and their confidence bounds (95%) for Model I and II are presented in Table 4. For Model I, parameter A estimates for aspen (A=7.59), hybrid spruce (A=3.784) and subalpine fir (A=9.35) results in probability of mortality close to 1 at zero relative radial growth. For lodgepole pine (A=0.098) the mortality at zero relative radial growth is much lower (~0.09) than for the other species resulting in a different shape of the mortality model (Figure 3). The decay rates in Model I with relative radial growth (parameter B estimates) were similar for aspen (B=187.84), hybrid spruce (B=195.30) and subalpine fir (B=197.96). Lodgepole pine has a much lower decay rate (B=37.81) than any of the other species, which probably owes to its relatively low probability of mortality at zero growth.

Table 4: Maximum likelihood estimates with 95% confidence bounds of model parameter estimates for the Full and reduced models (Model I and II) using absolute radial growth (a) and relative radial growth (b) as the predictor variable.

| Species | Model I ¹ | | Model II ¹ |
|----------------|-------------------------|---------------------------|---------------------------|
| | A | B | B |
| (a) | | | |
| Aspen | 0.07 (0.05-0.08) | 12.14 (10.87-13.45) | 29.85 (28.02-31.94) |
| Lodgepole pine | 0.02 (0.01-0.02) | 2.26 (1.62-2.97) | 18.75 (17.63-19.92) |
| Hybrid spruce | 0.06 (0.05-0.08) | 22.47 (19.85-25.76) | 43.86 (40.33-47.58) |
| Subalpine fir | 0.05 (0.04-0.06) | 18.63 (16.35-21.45) | 40.93 (37.89-44.19) |
| (b) | | | |
| Aspen | 7.594 (5.978-9.568) | 187.94 (180.46-195.65) | 128.70 (122.18-136.01) |
| Lodgepole pine | 0.098 (0.081-0.117) | 37.81 (33.47-42.19) | 99.37 (94.24-104.97) |
| Hybrid spruce | 3.784 (2.909-4.920) | 195.30 (184.56-206.94) | 150.50 (141.29-160.85) |
| Subalpine fir | 9.354 (7.231-12.005) | 197.96 (189.53-207.38) | 130.55 (122.95-138.93) |

¹ Model I: $m(g) = P\{X \leq t\} = 1 - \exp(-t \cdot A \cdot e^{-B \cdot g})$

Model II: $m(g) = P\{X \leq t\} = 1 - \exp(-t \cdot e^{-B \cdot g})$

Graphs of Model I with relative increment are presented in Figure 4. Between relative growth 0 and 0.024 the order of probability of mortality is (aspen = subalpine fir) > hybrid spruce > lodgepole pine. This changes between relative growth 0.024-0.028 where it is (aspen = subalpine fir) > lodgepole pine > hybrid spruce. Beyond a relative growth of 0.028 where the probability of mortality can be considered low for all species the order is lodgepole pine > (aspen = subalpine fir) > hybrid spruce. The shaded area in Figure 4 marks the relative radial growth area 0.01-0.03. The shape of the mortality functions in this area is very important for their predictions. The rapid increase of the probability of mortality means that trees which are predicted to grow this slow will likely be predicted to die within a few years. Thus the shape of the mortality functions correspond to the observations in the basic data: The majority of recently dead trees have grown in a certain relative radial growth interval prior to their death.

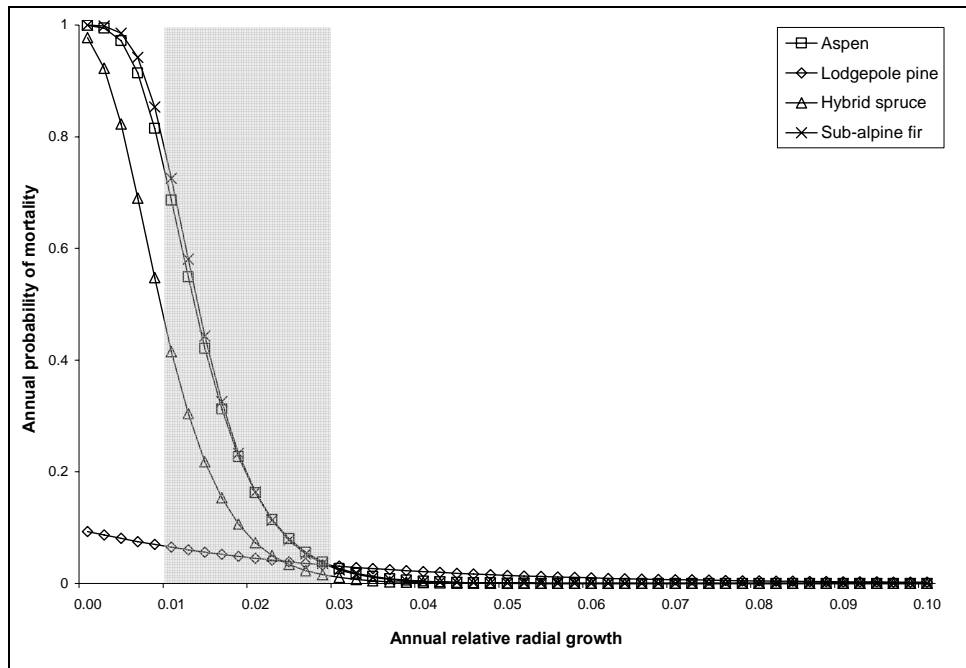


Figure 4: Probability of mortality as a function of recent annual relative radial growth (the arithmetic average of the five most recent complete years of radial growth). The graphs illustrate Model I with the maximum likelihood parameter estimates in Table 4. The shaded area is the relative radial growth interval 0.01-0.03.

To make a preliminary assessment of whether Model I with relative radial growth had a credible function form it was compared to the theoretical mortality function previously used in SORTIE-ND (Astrup and Larson 2005):

[Equation IX]
$$m(g) = z^{g / Max}$$

Here $m(g)$ is the annual probability of mortality, g is relative radial increment as defined above. Max and z (shape parameter) are user defined parameters. This model was derived from maximum density relationships found in simulations of pure stands of aspen, lodgepole pine, hybrid spruce and subalpine fir performed by the Tree and Stand Simulator (TASS) (Di Lucca 1999). Astrup and Larson (2005) found that this function contributed to acceptable thinning patterns, but that there was generally a slight overestimation of mortality. When specifically considering hybrid spruce and aspen they found that there was a tendency to overestimate mortality of both species. The comparison between empirical and theoretical mortality functions is presented in Figure 5.

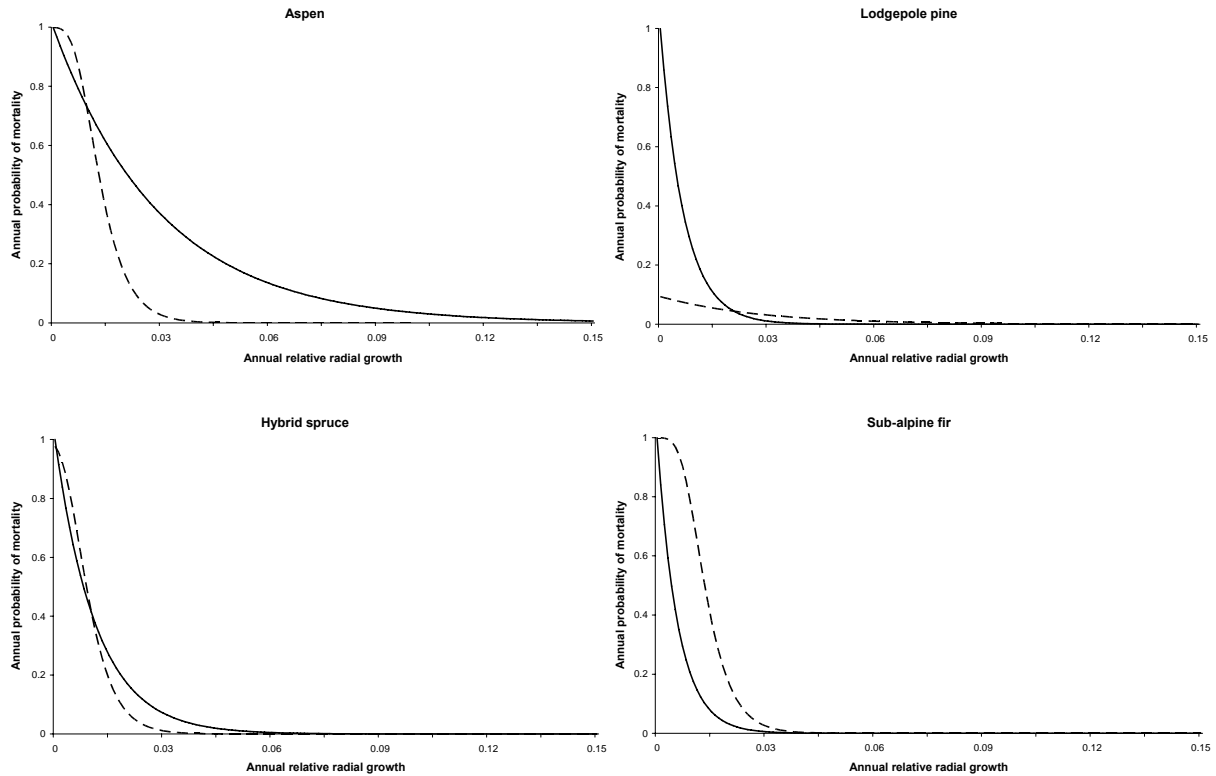


Figure 5: Empirical mortality functions (- - -) (Model I) compared to theoretical mortality models (—) previously used in SORTIE-ND.

The empirical mortality models conform to the general form of the theoretical models quite well. However, there are some discrepancies. The empirical model for lodgepole pine has much lower probabilities of mortality at low growth rates. At higher growth rates probability of mortality seems to be slightly higher. For aspen the empirical function decreases more abruptly and is generally lower. The empirical and theoretical functions for hybrid spruce have very similar shapes, but the empirical function has lower probability of mortality above 0.01 relative radial growth. The empirical mortality function for subalpine fir generally has a higher probability of mortality than the theoretical function.

Conditional plots of the mortality functions (Model I) show that tree size (DBH) will influence probability of mortality at a given level of absolute radial growth. In Figure 6, probability of mortality is depicted as a function of tree size (DBH) for each focal species and three levels of absolute radial growth. These plots were created by setting absolute radial growth to be constant in equation III. Consequently, relative radial growth (Equation III) and probability of mortality (Model I) are functions of tree size (DBH).

For aspen, lodgepole pine and hybrid spruce the conditional plots of the mortality models (Figure 6) indicate that probability of mortality will be highest at intermediate tree sizes at a given level of absolute radial growth. For subalpine fir probability of mortality increases until intermediate tree size after which it remains constant.

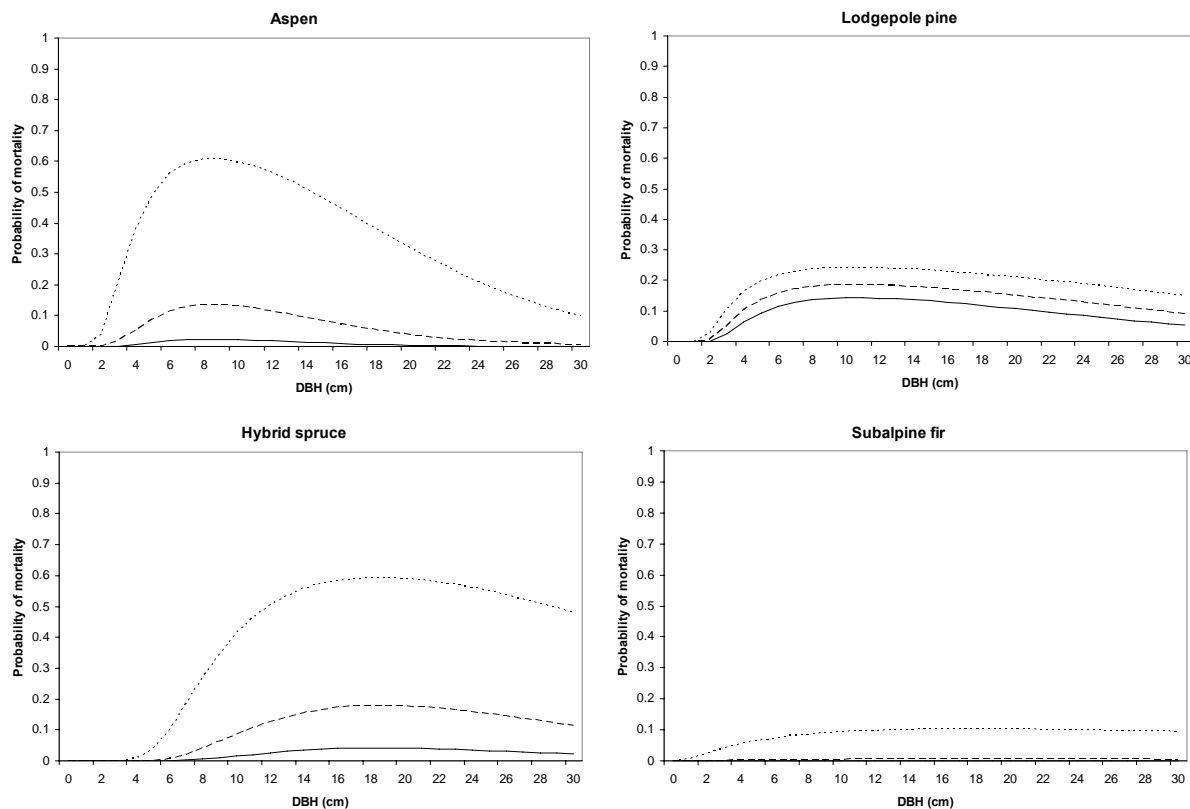


Figure 6: Conditional plots of the Full model for aspen, lodgepole pine, hybrid spruce and subalpine fir. Annual probability of mortality is shown as a function of tree size (DBH, cm) for three levels of absolute radial growth (---) 0.1 mm/yr, (---) 0.15 mm/yr and (—) 0.20 mm/yr.

Predictive ability of the mortality models

Qualitative model assessment

The new mortality functions were added to SORTIE-ND through a slight modification of the program code and the model parameters were specified through the model user interface. To assess the logic of the mortality functions and their self-thinning patterns, single species even-aged stands of the four focal species were simulated for different initial densities. The same simulations were performed with TASS for stand with a medium stand index (SI 21) and were drawn through TIPSYP (Table Interpolation Program for Stand Yield) which accesses stand yield tables produced by TASS. TASS is calibrated to permanent sample plot data and generally performs well when simulating even-aged stands of the focal species (Di Lucca 1999). An important feature of TASS is that it adheres to the Law of Constant Yield, meaning that irrespective of the initial density, stand density and basal area conform towards the same final values over time. Simulations of single species even-aged stands at three initial densities are presented in Figure 7 and 8.

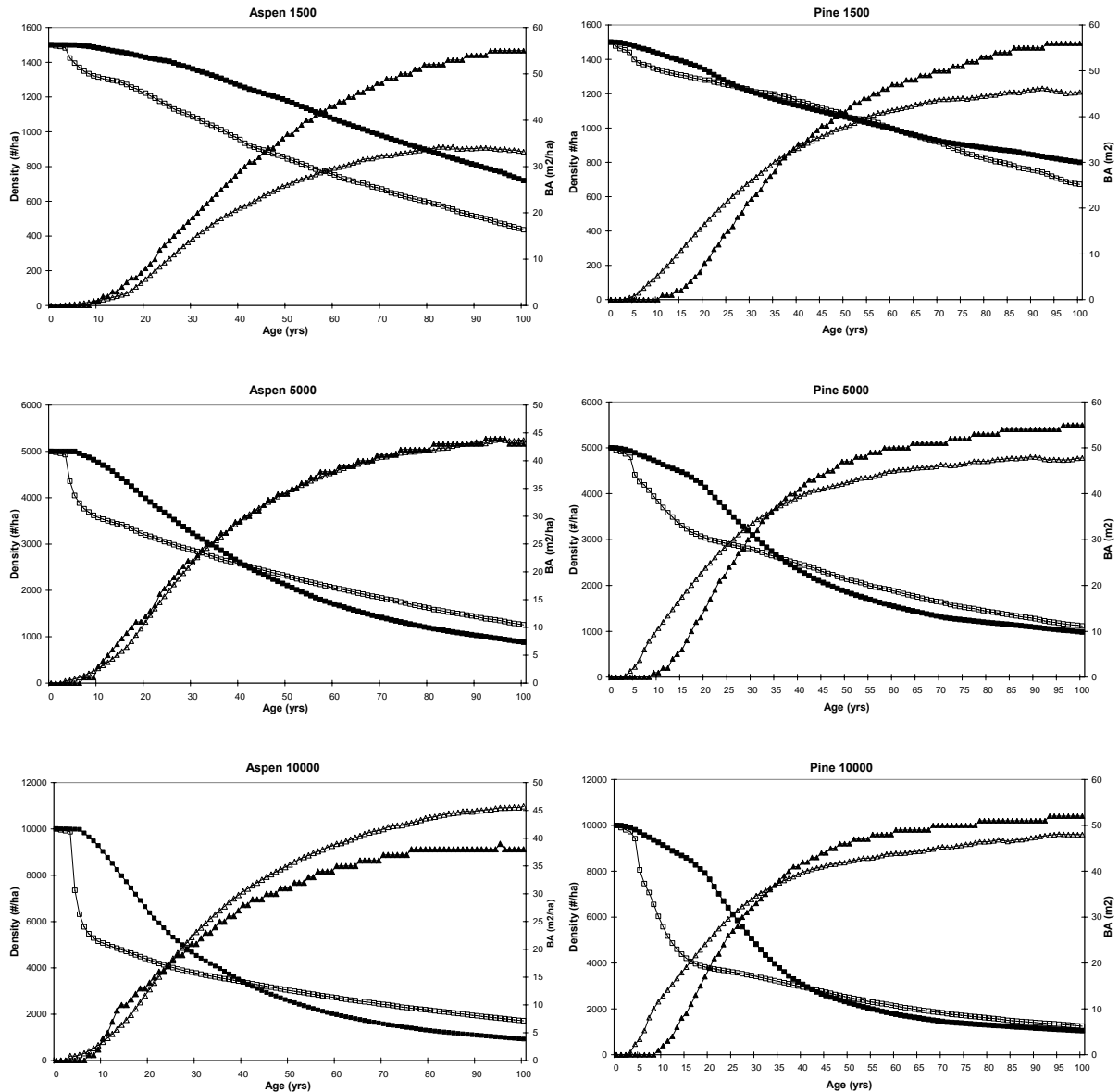


Figure 7: TIPSY (■ – Density, ▲ - Basal Area) and SORTIE-ND (□ - Density, Δ - Basal Area) simulations of pure even-aged stands of aspen and lodgepole pine with three different initial densities: 1500, 5000 and 10000 stems pr. ha. Predicted stand attribute are density and basal area.

For aspen Figure 7 shows that the two models produce very similar simulations for high initial densities (5000 and 10000 stems pr. ha). In the low initial density stand SORTIE-ND predicts considerably lower density and basal area at the end of the simulation. Additionally, SORTIE-ND has a very different self-thinning pattern than TIPSY. Density drops abruptly at an early age and then drops gradually through the rest of the simulation. The TIPSY simulations have more smooth self-thinning patterns, but also significantly higher self-thinning in the first half of the simulation.

For all initial densities of lodgepole pine TIPSY and SORTIE-ND generally produce similar results. SORTIE-ND produces slightly lower basal areas and it also has a self-thinning pattern with a slightly more abrupt drop in density at an early age than TIPSY.

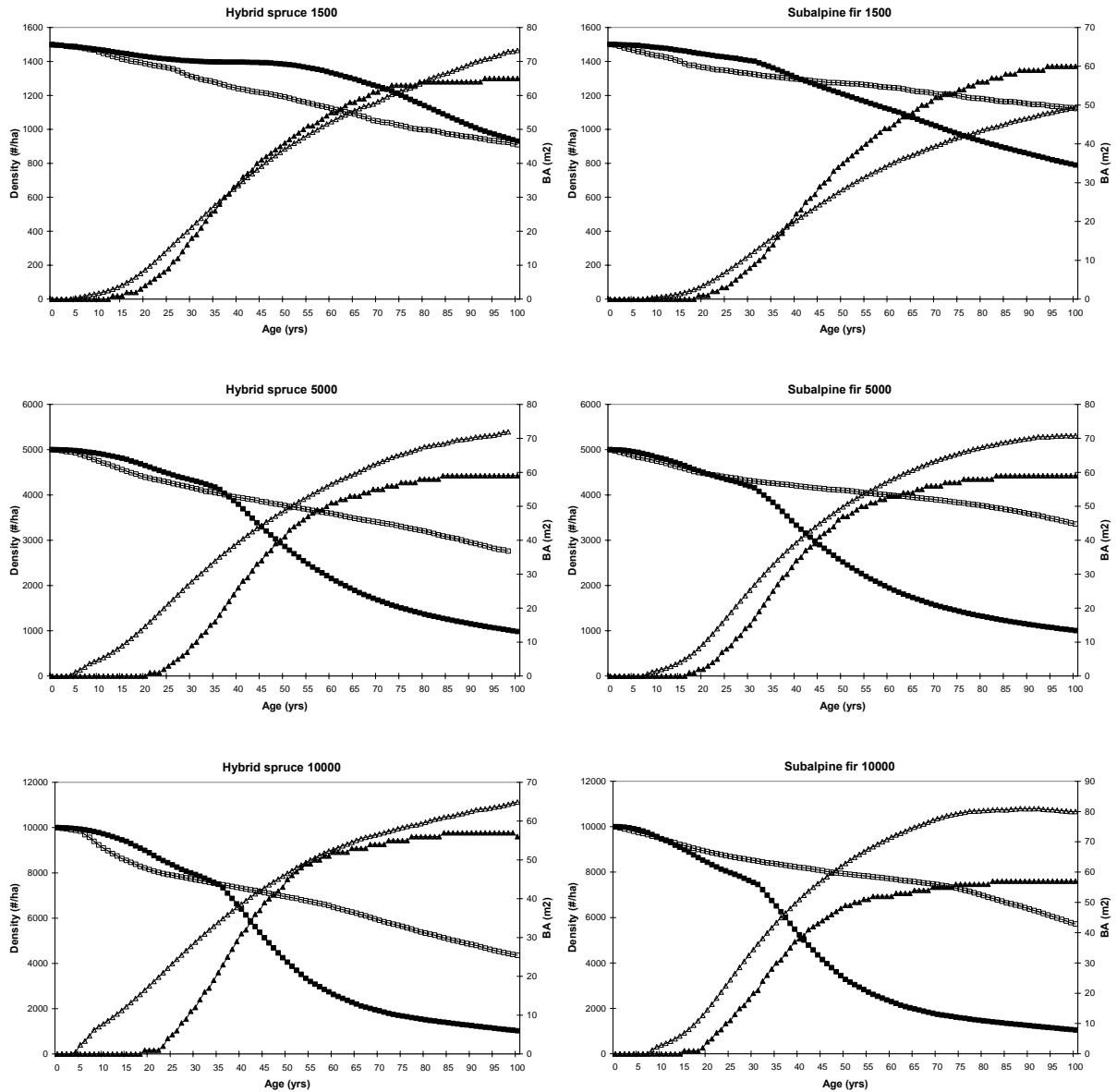


Figure 8: TIPSY (■ – Density, ▲ - Basal Area) and SORTIE-ND (□ - Density, Δ - Basal Area) simulations of pure even-aged stands of hybrid spruce and subalpine fir with three different initial densities: 1500, 5000 and 10000 stems pr. ha. Predicted stand attribute are density and basal area.

Figure 8 shows that hybrid spruce self-thins at a constant rate throughout the SORTIE-ND simulations of low and medium initial density stands. In the high initial density stand self-thinning is slightly higher until age 25, but levels out after that. TIPSY simulations show selfthinning patterns where stands start to selfthin more intensively midway through the simulation for medium and high initial densities and late in the simulation in the low initial density stand. Regardless of the initial density SORTIE-ND generally predicts very high basal areas throughout the simulations indicating that growth is generally overestimated.

Figure 8 shows that subalpine fir has a thinning pattern similar to hybrid spruce. In medium and high initial density stands, SORTIE-ND predicts much higher densities and basal areas than TIPSY. Based on Figure 7 and 8 general observations are summarized in Table 5.

Table 5: Summary of simulations of pure stands of aspen, lodgepole pine, hybrid spruce and subalpine fir performed with SORTIE-ND and TIPSy.

| | SORTIE-ND | TIPSy |
|-------------------------------|---|--|
| Thinning pattern | <ul style="list-style-type: none"> • Abrupt self-thinning at an early age followed by gradual reduction of stems. • Final density is dependent on initial density. | <ul style="list-style-type: none"> • Smooth and gradual reduction of stems. • Irrespective of initial density stands develop towards the same final density. |
| Basal area development | <ul style="list-style-type: none"> • Predicted basal area increases with initial density for aspen and subalpine fir. • Basal area is generally high for hybrid spruce and subalpine fir. • Final basal area is dependent initial density. | <ul style="list-style-type: none"> • Irrespective of initial density stands develop towards the same final basal area. |

To determine to which degree the new empirical mortality functions perform self-thinning, SORTIE-ND simulations were performed without the species specific random mortality functions. The results of these simulations are compared with simulations from Figure 7 in Figure 9. Only simulations of aspen and lodgepole pine are included. For aspen, random mortality accounts for a large portion of self-thinning especially in the low and medium initial density stands. This indicates that radial growth must be reduced considerably as an effect of competition for the new adult mortality functions to contribute to self-thinning. For lodgepole pine the random mortality function has a negligible influence on self-thinning in the medium and high initial density stands. In the low initial density stand the effect is more pronounced, but to a smaller extent than for aspen. The differences between aspen and lodgepole pine are to some extent a consequence of different random mortality rates. The random mortality rate for aspen is 1%, while it is 0.25% for lodgepole pine. For subalpine fir and hybrid spruce the random mortality rates were 0.25% and 0.50% respectively.

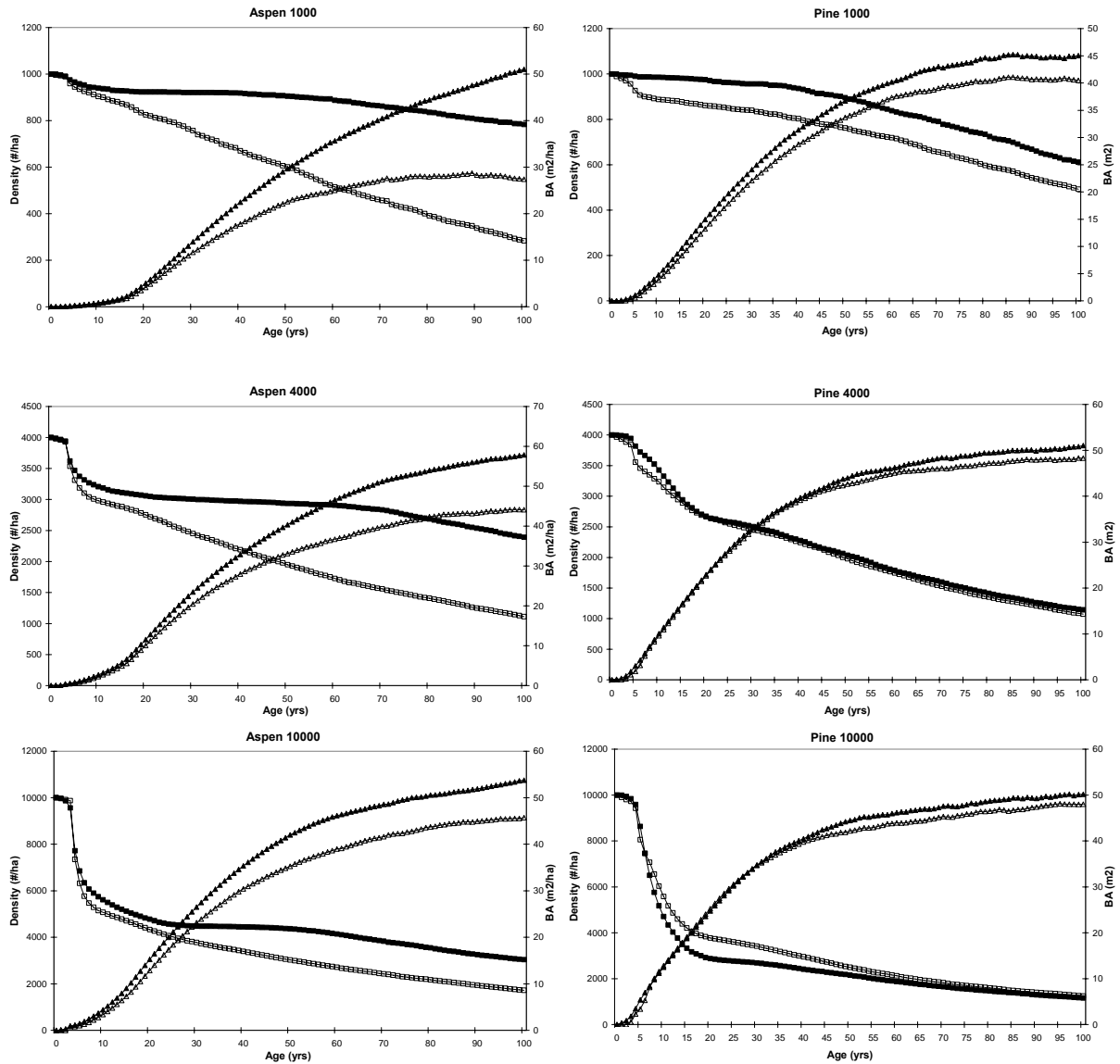


Figure 9: SORTIE-ND simulations of pure stands with and without random mortality functions. Simulations of pure even-aged stands of aspen and lodgepole pine with three different initial densities: 1000, 5000 and 10000 stems pr. ha. ■ - Density – without random mortality; □ - Density – with random mortality; ◆ - Basal Area – without random mortality; ◇ - Basal Area – with random mortality.

The influence of the random mortality functions on predicted stand density was also tested for complex stands. 30 year simulations of five permanent sample plots (stand 1-5 in appendix 1) containing aspen, lodgepole pine and hybrid spruce fir were performed with and without the random mortality function. All simulated trees in these stands had a DBH > 9.1 cm. In Table 6 two comparative statistics for the two simulations are presented: Residuals and the percentage of total mortality arising from the growth-based empirical mortality functions. Residuals are the species specific actual differences in predicted mortality between simulations with and without the random mortality functions. They are calculated at each 10 year time step according to:

$$Residual = \sum_x^{i=x+10} Mortality(w/ random mortality)_i - \sum_x^{i=x+10} Mortality(no random mortality)_i$$

The percentage of total mortality arising from the growth-based mortality functions in each 10 year time step was calculated according to:

$$\% \text{ growth-based mortality of total mortality} = \frac{\sum_{i=x+10}^x \text{Mortality}(\text{no random mortality})_i}{\sum_{i=x+10}^x \text{Mortality}(\text{w/ random mortality})_i} \times 100\%$$

Table 6: Statistic for comparison of SORTIE-ND simulations of five permanent sample plots (stand 1-5 in Appendix 1) with and without the random mortality function.

| Stand 1 | Residual ¹ | | | | % growth based mortality of total mortality ² | | | |
|---------|-----------------------|----------------|---------------|-------|--|----------------|---------------|-------|
| | Aspen | Lodgepole Pine | Hybrid Spruce | Total | Aspen | Lodgepole Pine | Hybrid Spruce | Total |
| Time | | | | | | | | |
| 10 | 90 | 1 | 14 | 105 | 9.6% | 89.6% | 0.0% | 12.0% |
| 20 | 83 | 0 | 14 | 97 | 9.9% | 100.0% | 0.0% | 16.1% |
| 30 | 68 | -0,2 | 12 | 80 | 17.1% | 101.8% | 0.9% | 25.1% |
| Stand 2 | Residual | | | | % growth based mortality of total mortality | | | |
| Time | Aspen | Lodgepole Pine | Hybrid Spruce | Total | Aspen | Lodgepole Pine | Hybrid Spruce | Total |
| 10 | 52 | 2 | 1 | 56 | 9.3% | 60.4% | 0.0% | 13.7% |
| 20 | 46 | 4 | 1 | 51 | 16.0% | 52.6% | 0.0% | 20.5% |
| 30 | 41 | 2 | 1 | 44 | 23.7% | 82.4% | 0.0% | 31.8% |
| Stand 3 | Residual | | | | % growth based mortality of total mortality | | | |
| Time | Aspen | Lodgepole Pine | Hybrid Spruce | Total | Aspen | Lodgepole Pine | Hybrid Spruce | Total |
| 10 | 23 | 5 | 1 | 30 | 15.0% | 44.9% | 0.0% | 22.1% |
| 20 | 20 | 6 | 1 | 27 | 26.1% | 52.6% | 0.0% | 33.9% |
| 30 | 16 | 3 | 1 | 20 | 42.4% | 76.1% | 0.0% | 52.2% |
| Stand 4 | Residual | | | | % growth based mortality of total mortality | | | |
| Time | Aspen | Lodgepole Pine | Hybrid Spruce | Total | Aspen | Lodgepole Pine | Hybrid Spruce | Total |
| 10 | 76 | 2 | 10 | 88 | 14.5% | 88.4% | 0.0% | 23.1% |
| 20 | 67 | 2 | 15 | 84 | 18.0% | 90.5% | 0.7% | 28.7% |
| 30 | 50 | -7 | 10 | 53 | 24.7% | 147.5% | 0.0% | 42.5% |
| Stand 5 | Residual | | | | % growth based mortality of total mortality | | | |
| Time | Aspen | Lodgepole Pine | Hybrid Spruce | Total | Aspen | Lodgepole Pine | Hybrid Spruce | Total |
| 10 | 30 | 6 | 11 | 47 | 14.0% | 54.5% | 0.0% | 19.7% |
| 20 | 27 | 4 | 13 | 44 | 17.2% | 70.8% | 1.7% | 26.8% |
| 30 | 19 | -2 | 13 | 30 | 34.9% | 111.9% | 0.8% | 46.9% |

$$1 \text{ Residual} = \sum_{i=x+10}^x \text{Mortality}(\text{w/ random mortality})_i - \sum_{i=x+10}^x \text{Mortality}(\text{no random mortality})_i$$

$$2 \text{ \% growth-based mortality of total mortality} = \frac{\sum_{i=x+10}^x \text{Mortality}(\text{no random mortality})_i}{\sum_{i=x+10}^x \text{Mortality}(\text{w/ random mortality})_i} \times 100\%$$

Table 6 shows that the random mortality function contributes significantly to mortality during the simulations. Due to higher random mortality rates for aspen and hybrid spruce (1% and 0.5%) the growth based mortality function account for 9.6 – 42.4% of total mortality for aspen and 0 – 1.7% of total mortality for hybrid spruce. For lodgepole pine, which has a

background mortality rate of 0.25%, the growth based mortality function accounts for 44.9 – 100 % of all mortality. In stands 1, 4 and 5 higher lodgepole pine mortality was predicted in the third time step when only using the growth based mortality function. This probably owes to an accumulation of suppressed trees at the end of the simulation which finally grow at a sufficiently slow rate to be affected by the growth based mortality function.

Quantitative model assessment

To test the predictive ability of the developed mortality functions in complex stands SORTIE-ND simulations of 51 permanent sample plots in the SBS in British Columbia were compared to remeasurements of the plots. Each of the permanent sample plots have been re-measured three times with 10 year intervals. The plots are located in uneven-aged mixed species stands. A summary of the sampled plots can be found in Appendix 1. Only trees larger than DBH = 9.1 cm were included in the analysis. In some of the plots there are small percentages of western paper birch (*Betula papyrifera* var. *commutata* (Regel) Fern.), black cottonwood (*Populus trichocarpa* Torr. & Gray) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). As data for these species was not accessible, birch and cottonwood were modelled as aspen and Douglas-fir was modelled as lodgepole pine. These species did not count as aspen and lodgepole pine in the summary statistics. When comparing SORTIE-ND predictions to the permanent sample plot data, it must be noted that errors can be due to both the growth functions and the mortality functions.

For aspen, Figure 1 (Appendix 2) illustrates 1:1 plots for the permanent sample plot data against model predictions. Figure 1 (Appendix 2) contains nine individual plots that illustrate aspen density, basal area and quadratic mean diameter at breast height (DBHQ) at each of the three re-measurements. Aspen density appears to follow the 1:1 line well for all three measurements. For basal area there appears to be a tendency for the model to slightly overestimate the basal area for stands with a basal area below 25m²/ha. Accordingly, there also appears to be a tendency of overestimation of DBHQ.

For lodgepole pine, Figure 2 (Appendix 2) illustrates 1:1 plots for permanent sample plot data against model predictions. Figure 1 (Appendix 2) contains nine individual plots that illustrate lodgepole pine density, basal area, and DBHQ at each of the three re-measurements. Predicted lodgepole pine densities are generally low. Nonetheless, the model density predictions and the observation follow the 1:1 line well. In terms of basal area and DBHQ the model seems to slightly underestimate the growth in the permanent sample plots.

For hybrid spruce, Figure 3 (Appendix 2) illustrates 1:1 plots for permanent sample plot data against model predictions. Figure 3 (Appendix 2) contains nine individual plots that illustrate spruce density, basal area, and DBHQ at each of the three re-measurements. For each of the three measurements, hybrid spruce density follows the 1:1 line well. The model overestimates basal area for stands with basal areas over 20m²/ha, and accordingly the DBHQ for these stands are also overestimated.

An evaluation of the subalpine fir model was not performed as there were insufficient amounts of subalpine fir in the permanent sample plots.

Summary statistic supplementing the visual assessment of model predictions compared to permanent sample plots are presented in Table 7. The accuracy of the predictions at each re-measurement is described by mean actual residual (bias). This is calculated according to:

$$\text{[Equation IX]} \quad \text{Mean Actual Residual} = \sum (\hat{y} - y) / n$$

Here \hat{y} and y are the predicted and observed basal area, density or DBHQ for a given species in each of the 51 permanent sample plots at each re-measurement. n is the number of plots which contain the specific species. The precision of the SORTIE-ND simulations can be expressed through the mean absolute residual. It is calculated according to the equation below which uses the same variables as Equation IX.

$$\text{[Equation X]} \quad \text{Mean Absolute Residual} = \sum \left| \hat{y} - y \right| / n$$

According to Vanclay and Skovsgaard (1997) the mean absolute residual is an efficient way to measure the average error for a single prediction. In conjunction with the mean actual residual this gives a summary of the overall model performance.

For aspen the summary statistics in Table 7 show that overall density, basal area and DBHQ are slightly overestimated. Thus, mortality is underestimated for aspen. For lodgepole pine basal area, density and DBHQ are generally underestimated, meaning that mortality is overestimated. Basal area and DBHQ are both overestimated for hybrid spruce, while predicted densities are slightly underestimated. Thus, mortality for spruce is overestimated. Very little data was available for subalpine fir. However the summary statistics show that basal area, density and DBHQ all were slightly overestimated, indicating that mortality is underestimated.

Table 7: Summary statistics for comparisons between measurements and SORTIE-ND simulations of 51 permanent sample plots in British Columbia containing aspen, lodgepole pine, hybrid spruce and subalpine fir.

| Aspen | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual ¹ | Mean Absolute Residual ² | Lodgepole pine | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual ¹ | Mean Absolute Residual ² |
|---------------|------|---------------------|----------------------|--------------|-----------------------------------|-------------------------------------|----------------|------|---------------------|----------------------|--------------|-----------------------------------|-------------------------------------|
| BA | 0 | 11.56 | | | | | BA | 0 | 5.68 | | | | |
| BA | 10 | 12.82 | 14.52 | 48 | 1.71 | 2.10 | BA | 10 | 6.97 | 6.34 | 47 | -0.63 | 0.90 |
| BA | 20 | 13.99 | 16.53 | 48 | 2.54 | 3.41 | BA | 20 | 7.80 | 6.57 | 47 | -1.23 | 1.69 |
| BA | 30 | 14.79 | 17.76 | 48 | 2.97 | 4.52 | BA | 30 | 8.60 | 6.48 | 47 | -2.12 | 2.58 |
| Density | 0 | 659.22 | | | | | Density | 0 | 165.92 | | | | |
| Density | 10 | 581.82 | 588.04 | 48 | 6.21 | 44.60 | Density | 10 | 152.81 | 151.99 | 47 | -0.82 | 11.35 |
| Density | 20 | 509.58 | 522.73 | 48 | 13.15 | 68.95 | Density | 20 | 145.13 | 135.78 | 47 | -9.35 | 17.36 |
| Density | 30 | 441.49 | 462.84 | 48 | 21.35 | 76.11 | Density | 30 | 136.39 | 118.56 | 47 | -17.83 | 23.93 |
| DBHQ | 0 | 15.03 | | | | | DBHQ | 0 | 22.52 | | | | |
| DBHQ | 10 | 17.14 | 18.12 | 48 | 0.99 | 1.40 | DBHQ | 10 | 26.07 | 24.79 | 47 | -1.28 | 1.61 |
| DBHQ | 20 | 19.27 | 20.61 | 48 | 1.35 | 2.28 | DBHQ | 20 | 28.37 | 26.54 | 47 | -1.82 | 2.30 |
| DBHQ | 30 | 21.29 | 22.73 | 48 | 1.44 | 3.05 | DBHQ | 30 | 30.56 | 27.99 | 47 | -2.56 | 3.12 |
| Hybrid Spruce | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual ¹ | Mean Absolute Residual ² | Subalpine fir | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual ¹ | Mean Absolute Residual ² |
| BA | 0 | 8.36 | | | | | BA | 0 | 1.17 | | | | |
| BA | 10 | 11.88 | 12.20 | 48 | 0.32 | 0.75 | BA | 10 | 1.54 | 1.67 | 14 | 0.13 | 0.17 |
| BA | 20 | 14.35 | 15.92 | 48 | 1.57 | 1.80 | BA | 20 | 1.82 | 2.18 | 14 | 0.37 | 0.41 |
| BA | 30 | 16.94 | 19.35 | 48 | 2.41 | 2.75 | BA | 30 | 2.00 | 2.68 | 14 | 0.67 | 0.73 |
| Density | 0 | 455.84 | | | | | Density | 0 | 60.74 | | | | |
| Density | 10 | 447.75 | 433.16 | 48 | -14.59 | 17.37 | Density | 10 | 60.03 | 59.10 | 14 | -0.93 | 2.30 |
| Density | 20 | 428.70 | 411.88 | 48 | -16.82 | 26.68 | Density | 20 | 56.15 | 57.42 | 14 | 1.28 | 3.30 |
| Density | 30 | 410.37 | 391.04 | 48 | -19.33 | 40.18 | Density | 30 | 49.44 | 55.71 | 14 | 6.28 | 8.77 |
| DBHQ | 0 | 15.44 | | | | | DBHQ | 0 | 15.63 | | | | |
| DBHQ | 10 | 19.20 | 19.86 | 48 | 0.66 | 0.93 | DBHQ | 10 | 17.52 | 19.12 | 14 | 1.60 | 1.92 |
| DBHQ | 20 | 22.35 | 23.86 | 48 | 1.51 | 1.82 | DBHQ | 20 | 19.62 | 22.35 | 14 | 2.73 | 3.18 |
| DBHQ | 30 | 25.23 | 27.49 | 48 | 2.26 | 2.72 | DBHQ | 30 | 21.73 | 25.35 | 14 | 3.62 | 4.13 |

$$^1 \text{ Mean Actual Residual} = \sum (\hat{y} - y) / n$$

$$^2 \text{ Mean Absolute Residual} = \sum |\hat{y} - y| / n$$

The summary statistic from the study by Astrup and Larson (2005) are shown in Table 8. Only species specific summary statistics for aspen and hybrid spruce were included in this study. This gives an opportunity to assess how the empirical mortality functions have affected the predictive abilities of SORTIE-ND for these two species. For aspen, mortality is underestimated with the empirical mortality function while it was overestimated with the theoretical function. This is quite logical since the empirical function generally had lower probability of mortality. Furthermore, with the empirical mortality function bias is smaller and precision has improved. Mortality is still overestimated to the same degree as with the theoretical function for hybrid spruce. Precision is slightly improved. This follows from Figure 5 as the shape of the empirical mortality function is very similar to the theoretical.

Table 8: Summary statistics for comparisons between measurements and SORTIE-ND simulations of 51 permanent sample plots in British Columbia containing aspen, lodgepole pine, hybrid spruce and subalpine fir. Adopted from Astrup and Larson (2005).

| Aspen | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual¹ | Mean Absolute Residual² |
|----------------------|-------------|----------------------------|-----------------------------|---------------------|---|---|
| BA | 0 | 11.56 | | | | |
| BA | 10 | 12.82 | - | 48 | 0.83 | 2.28 |
| BA | 20 | 13.99 | - | 48 | 0.91 | 3.56 |
| BA | 30 | 14.79 | - | 48 | 0.55 | 4.51 |
| Density | 0 | 659.22 | | | | |
| Density | 10 | 581.82 | - | 48 | -27.74 | 60.46 |
| Density | 20 | 509.58 | - | 48 | -45.72 | 80.45 |
| Density | 30 | 441.49 | - | 48 | -57.81 | 88.02 |
| DBHQ | 0 | 15.03 | - | 48 | | |
| DBHQ | 10 | 17.14 | - | 48 | 0.99 | 1.30 |
| DBHQ | 20 | 19.27 | - | 48 | 1.46 | 2.05 |
| DBHQ | 30 | 21.29 | - | 48 | 1.73 | 2.75 |
| Hybrid Spruce | Year | Mean Observed Value | Mean Predicted Value | No. of Plots | Mean Actual Residual¹ | Mean Absolute Residual² |
| BA | 0 | 8.36 | | | | |
| BA | 10 | 11.88 | - | 48 | 0.36 | 0.74 |
| BA | 20 | 14.35 | - | 48 | 1.66 | 1.83 |
| BA | 30 | 16.94 | - | 48 | 2.64 | 2.86 |
| Density | 0 | 455.84 | | | | |
| Density | 10 | 447.75 | - | 48 | -14.88 | 17.31 |
| Density | 20 | 428.70 | - | 48 | -18.07 | 25.68 |
| Density | 30 | 410.37 | - | 48 | -22.18 | 36.99 |
| DBHQ | 0 | 15.44 | | | | |
| DBHQ | 10 | 19.20 | - | 48 | 0.69 | 0.91 |
| DBHQ | 20 | 22.35 | - | 48 | 1.58 | 1.83 |
| DBHQ | 30 | 25.23 | - | 48 | 2.42 | 2.80 |

$$^1 \text{ Mean Actual Residual} = \sum (\hat{y} - y) / n$$

$$^2 \text{ Mean Absolute Residual} = \sum | \hat{y} - y | / n$$

Discussion

Field method

The selected field method provides a straight forward approach to obtaining empirical data for parameter estimation. The major difficulty during field sampling was to find stands with sufficient self-thinning and a large sample of recently dead trees. Density dependent mortality levels off with stand age meaning that sampling of older stands and larger trees becomes increasingly demanding, *i.e.* very large plots are needed to obtain a sufficiently large sample of recently dead trees.

The most questionable part of the sampling method is related to determining which trees are recently dead. The assessment of recently dead trees was subjective, which increases the risk for inconsistencies and makes it difficult to formally evaluate its accuracy. Since the formally tested recently dead criteria of Bartemucci and Coates (unpublished manuscript) were adopted in this study the field assessments have a solid foundation. The field assessments were primarily based on whether dead trees had retention of foliage. Missing foliage indicates that trees have been dead for at least 2-3 years, which means that the number of recently dead trees in a stand may have been underestimated. However, since the less accurate crown intactness criteria also were utilised extensively there is a risk that too old trees were classified as recently dead. Consequently, the number of recently dead trees can be expected to be quite accurate. All stands had obviously been in the stem exclusion stage for an extended period. Since dead trees from older mortality were still present in the stand, there was a good reference for the assessment of recently dead trees and a very small classification error can be expected.

Newbery *et al.* (2004) constructed models for estimating time since death for hybrid spruce and subalpine fir. The models were able to predict time since death as far back as 70 years. All predictor variables related to the degree of decay of different parts of the tree. The longevity of measurability of the predictor variables was found to be important for the period they gave reasonable predictions for. Newbery *et al.* (2004) confirmed that foliage retention and crown intactness are valuable predictor variables for time since death in the short term. The use of bark attachment and bark class was found to work better for older mortality. This implies that our emphasis on foliage retention and crown intactness is likely to give satisfactory predictions when the recently dead period is 5 years.

Another disadvantage with the current field method is that it does not account for site variation. Especially variation in soil moisture is believed to have an influence on the process of mortality (Kobe *et al.* 1995, Kobe 1996, Kobe and Coates 1997). It is commonly accepted that in even-aged stands mortality sets in at an earlier stage and increases with site productivity. By primarily sampling sites with mesic moisture and medium nutrient regimes the aim was to produce general models. Pooling all sampling sites possibly accounted for some between-site variation and potentially improved the generality of the models. Collecting a sample big enough to incorporate site effects in the present types of models would require an overwhelming sampling effort.

Predictor variable selection

It was clear from the field data that relative radial growth was a better predictor of mortality than absolute radial growth. In previous studies using the same basic method of model development (Kobe *et al.* 1995, Kobe 1996, Kobe and Coates 1997) relative radial growth has not been tested, but absolute radial growth proved to be a sufficient predictor of mortality. Since variation in tree size was very small ($DBH < 5$ cm) in these studies there was hardly any to need to account for this.

Using a different modelling approach Wyckoff and Clark (2000) also used recent radial growth as the predictor of mortality for adult trees. The models did not account for tree size. They failed to capture increasing probability of mortality at low growth, but performed well at higher growth rates. Bigler and Bugmann (2004) and Bigler *et al.* (2004) found that including tree size in their empirical individual tree mortality models for Norway spruce and silver fir improved the predictive abilities. Furthermore, in stand-level mortality models tree size has also often been found to be a useful predictor of mortality (e.g. Monserud 1976, Buchman *et al.* (1983), Eid and Tuhus (2001), Fridman and Ståhl (2001), Yang *et al.* (2003)). Thus, there is considerable support for incorporating tree size into mortality models. This probably relates to the physiological relationship between radial growth and tree size.

For saplings of southern boreal species in Quebec, Kneeshaw *et al.* (2006) found that probability of mortality increases with sapling size except for the most shade intolerant species aspen. This was explained by ontogenetic shifts inhibiting adaptation to suppression and a larger demand from maintenance respiration with increasing tree size. The findings of Kneeshaw *et al.* (2006) correspond well to the mortality models developed in this study. The conditional plots of the mortality models (Figure 6) also show that for small trees ($DBH < 10$ cm) probability of mortality increases with tree size.

The relationship between tree size and tolerance to low growth for the four focal species is illustrated in Figure 6. This relationship is an effect of the relation between potential growth and trees size determined by Canham *et al.* (2004). High probability of mortality is an expression of low tolerance to low growth. For aspen, lodgepole pine and hybrid spruce probability of mortality at a given level of absolute radial growth increases until intermediate trees size ($DBH = 10-15$ cm) and then decreases as trees grow larger. For subalpine fir probability of mortality increases with tree size until intermediate tree size and remains high with increasing tree size. The initial increase in probability of mortality with tree size is an effect of an increasing demand from maintenance respiration: As an effect of increasing proportion of photosynthetic tissue trees can potentially grow faster as their size increases. However, the demand from maintenance respiration means that if a larger tree relatively speaking is growing slower, it will have lower vigour and higher probability of mortality. A large tree which is growing at the same absolute radial growth rate as a small tree will have a lower relative radial growth, can allocate less photosynthates to maintain and expand its biomass and will have lower vigour (*i.e.* higher probability of mortality). Beyond a certain tree size potential radial growth will start to decrease: Trees will not be able to expand biomass production infinitely because the amount of photosynthetic in relation to respiring tissue reaches a maximum. Additionally, when diameter increases a small radial increment equals a large basal area increment. Consequently, maximum potential radial growth may decrease while maximum basal area increment remains constant or decreases at a slower rate. A large tree which grows at the same absolute radial growth rate as tree of intermediate size will grow faster relatively speaking and have a lower probability of mortality. Subalpine fir does not follow the pattern with decreasing probability of mortality for large trees. Since

subalpine fir is a very shade tolerant species it can retain a deep crown for longer and can potentially expand its photosynthetic tissue more than the other species. Therefore it can maintain a high potential radial growth for longer and large trees will have a higher probability of mortality at a given absolute radial growth rate than small trees.

Only short term recent radial growth was used for mortality predictions in the present study. Indications that a combination of short term tree growth level, long term growth trend and relative growth yield satisfactory mortality models (Bigler and Bugmann 2003) could have motivated the use of long term growth data as well. Dying trees are often characterized by having low growth levels (short term growth), declining long term growth trends and very low relative growth (Bigler *et al.* 2004). Basing mortality models on recent growth alone is in all probability less certain as long term growth data shows that trees can adapt to conditions resulting in low growth. However, mortality models based on long term growth data requires more extensive sampling efforts and laboratory analyses.

The inclusion of further predictor variables in the empirical mortality functions would possibly improve their predictive abilities further. Additional predictor variables were not considered because of the relatively straight forward approach of the adopted field method and basic models. In addition the current field method would be hampered by sampling routines for other predictor variables such as competition and crowding indexes (e.g. He and Duncan 2000) or crown attributes of individual trees (Fan *et al.* 2006, Keane *et al.* 1999). Finally using growth as a predictor of mortality in the SORTIE-ND framework indirectly includes competition because growth is predicted from the neighbourhood competition index (NCI).

Qualitative model assessment

The new empirical mortality functions showed to improve the predictive abilities of SORTIE-ND. In comparison to the theoretical mortality function used by Astrup and Larson (2005), for aspen and hybrid spruce, the empirical functions generally had lower probabilities of mortality. In relation to the comparison to permanent sample plots by Astrup and Larson (2005), this was a promising result, as the theoretical functions were found to contribute to overestimation of mortality for aspen and hybrid spruce.

Compared to the theoretical mortality function the empirical mortality function for lodgepole pine had very low probability of mortality at low growth rates but higher at intermediate to high growth rates. The model discrepancies at low growth rates probably have negligible influence on the predictive abilities. Generally, the predicted mortality at low relative growth (0-0.01) is of little influence on the overall performance of the mortality models as few trees grow this slow in the field data (aspen: 0, lodgepole pine: 10, hybrid spruce: 0 and subalpine fir: 5). A number of the live sampled lodgepole pine were observed to have very low growth levels. This probably explains why probability of mortality at low growth was estimated to be much lower for lodgepole pine than the other species. Overall, the model still assigns significantly higher probabilities of mortality to slow growing trees and causes effective self-thinning.

The empirical mortality function for subalpine fir had higher probability of mortality than the theoretical. As subalpine fir is a shade-tolerant species it can be expected that it has low probabilities of mortality in line with the theoretical function. Thus, it is possible that the

empirical functions overestimate mortality. Nonetheless the simulations of pure stands did not indicate that this was the case.

The SORTIE-ND long term simulations of pure stands showed that the model has significant variation among species in thinning patterns and growth predictions. For aspen there is a tendency predict high basal area at intermediate and high initial densities compared to TIPSY simulations. For low initial densities of aspen, density is probably underestimated somewhat. In the SORTIE-ND simulations of aspen, very intensive self-thinning at an early age is followed by a more moderate reduction of stems. Juvenile mortality functions account for the early self-thinning, which means that the new empirical functions perform a more gradual reduction of stems. The gradual thinning pattern corresponds well to the thinning pattern found in the TIPSY simulations. SORTIE-ND simulations were also performed on stands with very high initial densities (10000-250000 stems/ha). Peterson and Peterson (1995) presented empirical data for such high stand densities which shows a steeper decline in stand densities than in SORTIE-ND simulations. Furthermore SORTIE-ND predicts somewhat high final densities at high initial densities compared to TASS simulations and the empirical data (Peterson and Peterson 1995). This indicates that SORTIE-ND with the new mortality functions underestimates density dependent mortality. This may very well be caused by overestimation of radial growth by the aspen growth function, even at very high densities where competition is intense.

The lodgepole pine simulations generally correspond well to the TIPSY simulations and have realistic thinning patterns. Still there is a tendency for a very sharp reduction of stems at an early age, which would probably not occur in natural stands. However this is caused by the juvenile mortality function rather than the adult tree mortality function.

For both hybrid spruce and subalpine fir the empirical mortality functions seem to underestimate mortality at higher initial densities, as both final densities and basal areas are significantly higher than in the TIPSY simulations. TIPSY simulations of stands with a high initial density (>3000 stems/ha) should be treated with some caution because the underlying TASS model only was calibrated to stands with lower densities (Astrup pers. comm.). Furthermore the TASS model was not calibrated to data for subalpine fir. Rather subalpine fir is modelled as hybrid spruce with a theoretical correction. SORTIE-ND does not drastically reduce stem numbers at an early age for these two species. Stands are thinned at a rate somewhat slower than what could be expected. Consequently, it seems that the onset of density dependent mortality is not properly depicted by the new mortality models. Another explanation for the lack of self-thinning is that the growth functions for both species generally overestimate radial growth. This was a problem for hybrid spruce indicated by Astrup and Larson (2005).

SORTIE-ND is designed for mixed-species uneven-aged stands with more complex structures. In even-aged single species stands, SORTIE-ND likely suffers from not inferring differentiated height growth in a stand of individuals that essentially are the same from the beginning of the simulation. Thereby each tree more or less experiences the same conditions and grows at almost the same rate as its neighbours. Gradually the random mortality function introduces different condition across the stand, but pronounced density dependent mortality is delayed. In complex stands differentiation and variation between individuals is much greater, due to age and species differences. The comparison to the 51 permanent sample plots consequently gives a better picture of how the new mortality functions have altered the predictive abilities of SORTIE-ND. The fact that the empirical mortality functions tend to

predict lower probability of mortality for aspen, spruce and subalpine fir indicates that they will work better than the theoretical mortality functions.

Quantitative model assessment

The 1:1 plots of predicted growth and mortality versus observed growth and mortality (Appendix 2, Figure 1-3) indicate: (1) The simulations of mixed stands showed that predicted aspen, lodgepole pine and hybrid spruce densities were generally in agreement with the observed values. (2) Growth is overestimated somewhat for aspen and hybrid spruce and underestimated for lodgepole pine.

In general, residuals for basal area and DBHQ show that growth is still overestimated, but that the precision has improved. This strengthens the conclusion drawn from the qualitative model assessment: The mortality functions give lower probabilities of mortality and result in realistic thinning patterns for intermediate initial densities. Generally the new functions seem to have improved the predictive abilities of SORTIE-ND for mixed stands. However, the individual species must to be considered separately.

The summary statistics (Table 7) show that aspen mortality is underestimated. Aspen mortality was overestimated with the theoretical mortality function. The empirical function underestimates because probability of mortality generally is lower than in the theoretical function and because growth is overestimated. The growth model in SORTIE-ND most likely overestimates growth of aspen because it was parameterized from empirical data collected at too rich sites (Astrup pers. comm.). However, the empirical mortality function has resulted in smaller bias and better precision. In conclusion, the empirical mortality function for aspen has improved the predictive abilities of SORTIE-ND and gives satisfactory predictions of mixed species stands.

For hybrid spruce, mortality is still overestimated to the same extent with the empirical mortality function. The simulations of even-aged stands also showed that SORTIE-ND tends to predict high mortality for medium and high initial density stands. Considering the average spruce density in the modelled permanent sample plots and the precision of the density predictions (e.g. much higher than for aspen), the overestimation is not severe. The shape of the empirical mortality function is very similar to the theoretical function which means changes in predictions should be marginal. Growth is overestimated for hybrid spruce. This is also an effect of growth model parameterization from empirical data collected at too rich sites (Astrup pers. comm.). An overestimation of growth should lead to an underestimation of mortality as a high radial growth rate will result in a lower probability of mortality. Thus, there seems to be a discrepancy between the growth model and the mortality model for hybrid spruce in SORTIE-ND. A likely explanation for the slight overestimation of mortality for hybrid spruce is that the random mortality rate of 0.50% is too high. Residuals in Table 6 showed that random mortality accounts for nearly all hybrid spruce mortality in the five modelled permanent sample plots. Consequently, the random mortality rate should be lower and the growth model should predict lower growth rates for the empirical mortality function to work properly.

In the study by Astrup and Larson (2005) statistics for lodgepole pine and subalpine fir were not summarized, ruling out quantitative comparisons. The lodgepole pine summary statistics indicate that mortality is overestimated, while growth is underestimated. The basic

relationship between radial growth rate and probability of mortality (Figure 4) explains this. Even though the lodgepole pine mortality functions perform well with respect to bias and precision the predictive abilities of SORTIE-ND could be improved by an improved growth function.

It is not possible to make quantitative comparisons for subalpine fir either. Furthermore subalpine fir was only present in 13 of the permanent sample plots and at low densities, making it difficult to draw any conclusions for the summary statistics. What the summary statistic indicate is that growth is overestimated and mortality is underestimated. Parameterization of the subalpine fir growth function from data collected at productive sites could explain this.

Random mortality

Even though the new mortality functions generally have contributed to improving predictions of mixed species stands it is important to note that the species specific random mortality rates play an important part in producing precise predictions of mortality. Mortality is a highly stochastic process that cannot only be described by correlations between probability of mortality and measures of tree growth and tree size. This was shown through simulations of both pure and mixed species stands (Figure 8 and Table 4).

The growth based mortality functions only account for part of the total mortality. The empirical approach chosen in this study focuses exclusively on the relation between relative growth and mortality. It is obvious that the empirical mortality functions must be supplemented with functions that can account for other factors inducing mortality. Thus setting the random mortality rate appropriately will have a large influence on model performance. This was evident from the quantitative assessment of the empirical mortality functions for hybrid spruce. Growth based mortality functions are very dependent on the predictive abilities of the underlying growth models. An over- or underestimation of growth obviously leads to biased mortality predictions even if the mortality models otherwise give precise prediction. To some degree this hampers testing model performance through SORTIE-ND simulations. To make an independent test of the mortality functions they could be tested on actual tree growth rather than predicted growth.

Conclusion

The tests of the mortality models in SORTIE-ND showed that they contribute to realistic thinning patterns in both simulations of single species even-aged stands and complex stands. Accounting for tree size in the mortality models gave better fits to the field data used for parameterization than using absolute radial growth as the predictor of mortality. Tolerance to low growth decreases to a minimum at intermediate trees size for all species except for subalpine fir, where it decreases and remains low as trees grow larger. This is an effect of the ontogenetic characteristics of the individual species. Overall, the tested method provides a straight forward approach to parameterizing growth based mortality models from field data which is relatively easy to obtain.

It was evident that the performance of the mortality models is highly dependent on the underlying growth models as well as mortality models accounting for random mortality. In simulations of complex stands the tendency to underestimate lodgepole pine mortality is caused by a slight overestimation of growth. Low aspen and subalpine fir mortalities are a consequence of an underestimation of growth. For hybrid spruce overestimation of mortality is more likely an effect of a high random mortality rate. Both growth functions and random mortality rates in SORTIE-ND should be improved. Still, the general performance of SORTIE-ND in complex stands makes it an appropriate management support tool.

Appendix 1

Stand summary statistics for the 51 permanent sample plots. The species codes are: aspen (At), lodgepole pine (PI), hybrid spruce (S), subalpine fir (BL), birch (Ep), cottonwood (Ac), Douglas-fir (Fd). Site index is estimated for the leading species at 50 years of age at dbh.

| Stand | BEC classification | Plot Size (ha) | Year Est. | Species Composition (Species code %cover) | Age (yrs) | Site Index | Volume (m ³ /ha) | Basal Area (m ² /ha) | Density (stems/ha) |
|-------|--------------------|----------------|-----------|---|-----------|------------|-----------------------------|---------------------------------|--------------------|
| 1 | SBS mw 01 | 0.081 | 70 | At 44 PI 42 S 14 | 30 | 18.2 | 110 | 17.9 | 1383 |
| 2 | SBS mw 03 | 0.081 | 70 | PI 52 At 45 S 03 | 30 | 20.6 | 83 | 13.0 | 716 |
| 3 | SBS mk 1 05 | 0.101 | 71 | At 53 PI 47 | 32 | 19.2 | 85 | 13.0 | 515 |
| 4 | SBS mk 1 01 | 0.101 | 71 | At 71 PI 16 S 13 | 39 | 20 | 211 | 29.8 | 1228 |
| 5 | SBS mk 1 01 | 0.101 | 71 | At 45 PI 37 S 18 | 31 | 20.6 | 152 | 21.2 | 733 |
| 6 | SBS mk 1 01 | 0.101 | 71 | At 96 S 02 PI 01 Ep 01 | 40 | 18.9 | 119 | 18.3 | 1109 |
| 7 | SBS mk 1 05 | 0.101 | 71 | PI 75 At 25 | 32 | 17.4 | 84 | 13.5 | 911 |
| 8 | SBS mk 1 01 | 0.101 | 71 | At 53 PI 29 S 18 | 41 | 16.9 | 129 | 19.7 | 1099 |
| 9 | SBS mk 1 01 | 0.101 | 71 | At 70 PI 21 S 07 Ep 02 | 37 | 18.2 | 125 | 18.5 | 1010 |
| 10 | SBS mk 1 01 | 0.101 | 71 | PI 53 At 30 S 14 Ep 03 | 37 | 18.4 | 134 | 19.8 | 970 |
| 11 | SBS mk 1 01 | 0.081 | 71 | At 46 S 42 Ep 10 PI 02 | 37 | 16.2 | 104 | 20.8 | 1556 |
| 12 | SBS mk 1 01 | 0.101 | 71 | At 38 PI 31 S 31 | 36 | 18.9 | 159 | 24.3 | 1040 |
| 13 | SBS mk 1 05 | 0.101 | 71 | At 43 S 29 PI 24 Ep 02 Bl 02 | 32 | 19 | 149 | 25.4 | 1525 |
| 14 | SBS mk 1 01 | 0.101 | 71 | At 65 PI 21 S 08 Ep 06 | 37 | 17 | 169 | 26.6 | 1248 |
| 15 | SBS mw 01 | 0.101 | 71 | PI 77 At 20 S 03 | 23 | 17 | 66 | 11.1 | 733 |
| 16 | SBS mw 01 | 0.101 | 71 | At 61 PI 39 | 35 | 22.2 | 154 | 22.8 | 1188 |
| 17 | SBS mw 01 | 0.101 | 71 | PI 54 At 40 S 06 | 37 | 17.5 | 141 | 20.7 | 1287 |
| 18 | SBS mw 01 | 0.101 | 71 | At 58 S 42 | 37 | 19.8 | 101 | 17.2 | 1089 |
| 19 | SBS mw 01 | 0.101 | 71 | At 77 S 19 PI 04 | 19 | 20.6 | 103 | 19.5 | 1010 |
| 20 | SBS wk 2 01 | 0.101 | 71 | At 54 PI 46 | 41 | 20.4 | 248 | 29.4 | 1337 |
| 21 | SBS mk 1 01 | 0.101 | 71 | PI 63 At 32 Ac 05 | 28 | 19.7 | 58 | 10.7 | 851 |
| 22 | SBS mk 1 01 | 0.101 | 71 | PI 54 At 44 Bl 02 | 30 | 22.4 | 92 | 14.0 | 941 |
| 23 | SBS mk 2 01 | 0.101 | 71 | At 62 PI 36 Ep 02 | 41 | 23.1 | 238 | 29.3 | 1832 |
| 24 | SBS wk 2 01 | 0.101 | 71 | At 74 PI 25 S 01 | 44 | 18.3 | 301 | 40.3 | 2297 |
| 25 | SBS wk 2 01 | 0.101 | 71 | At 39 S 27 Bl 22 PI 07 Ac 05 | 38 | 18.7 | 151 | 24.1 | 1762 |
| 26 | SBS wk 2 01 | 0.101 | 71 | At 49 PI 43 S 08 | 53 | 17.9 | 257 | 31.5 | 1891 |
| 27 | SBS wk 2 01 | 0.081 | 71 | At 86 S 08 PI 06 | 49 | 23.4 | 329 | 40.8 | 1667 |
| 28 | SBS wk 2 01 | 0.081 | 71 | At 76 S 24 | 49 | 23.7 | 294 | 39.9 | 1728 |
| 29 | SBS mk 2 03 | 0.081 | 71 | At 49 PI 31 S 17 Ep 01 Ac 02 | 61 | 17.5 | 366 | 47.4 | 1605 |
| 30 | SBS mk 1 01 | 0.101 | 71 | At 86 Ep 10 PI 03 S 01 | 37 | 22.7 | 128 | 20.4 | 1505 |

| | | | | | | | | | |
|----|-------------|-------|----|------------------------------|----|------|-----|------|------|
| 31 | SBS mk 1 03 | 0.101 | 71 | PI 95 At 05 | 34 | 15.2 | 25 | 3.8 | 277 |
| 32 | SBS mw 01 | 0.081 | 71 | S 58 PI 38 BI 04 | 79 | 17.3 | 245 | 37.2 | 2235 |
| 33 | SBS mw 01 | 0.101 | 71 | S 67 PI 16 At 13 Ep 04 | 65 | 24.9 | 120 | 16.5 | 347 |
| 34 | SBS dw 1 01 | 0.081 | 71 | S 85 BI 10 PI 05 | 74 | 21.3 | 274 | 36.8 | 1802 |
| 35 | SBS mw 01 | 0.081 | 70 | S 49 PI 34 At 14 Fd 03 | 59 | 21.7 | 147 | 22.8 | 852 |
| 36 | SBS mw 01 | 0.081 | 70 | S 56 At 26 PI 18 | 59 | 21.3 | 152 | 25.7 | 1321 |
| 37 | SBS mw 01 | 0.081 | 70 | S 46 PI 30 At 24 | 58 | 22.3 | 122 | 17.4 | 519 |
| 39 | SBS mk 1 01 | 0.101 | 71 | S 41 PI 37 At 22 | 63 | 20.1 | 169 | 26.4 | 1069 |
| 40 | SBS mk 1 01 | 0.101 | 71 | S 42 PI 36 At 17 BI 05 | 57 | 18.2 | 114 | 20.4 | 1416 |
| 41 | SBS mk 1 01 | 0.081 | 71 | S 54 PI 26 At 13 BI 05 Fd 02 | 72 | 20 | 210 | 31.6 | 1370 |
| 42 | SBS mk 1 05 | 0.081 | 71 | S 45 PI 39 At 12 BI 02 Fd 02 | 72 | 17.9 | 186 | 29.5 | 1284 |
| 43 | SBS mk 1 05 | 0.101 | 71 | S 60 PI 30 At 07 Fd 03 BI | 69 | 20.5 | 188 | 26.4 | 881 |
| 44 | SBS mw 01 | 0.101 | 71 | S 90 At 06 PI 04 | 67 | 18.5 | 102 | 23.4 | 1168 |
| 45 | SBS mw 01 | 0.101 | 71 | S 56 PI 23 At 21 W tr | 65 | 21.1 | 130 | 21.9 | 1238 |
| 46 | SBS mw 01 | 0.101 | 71 | S 50 PI 47 Fd 02 Ep 01 | 66 | 22.9 | 218 | 30.8 | 1267 |
| 47 | SBS mw 01 | 0.101 | 71 | S 90 PI 06 Fd 03 At 01 | 60 | 21.9 | 138 | 27.1 | 1030 |
| 48 | SBS mw 01 | 0.101 | 71 | S 82 At 17 Fd 01 | 60 | 20.7 | 121 | 22.4 | 1079 |
| 49 | SBS mw 01 | 0.101 | 71 | S 64 At 25 PI 07 Fd 04 | 70 | 20.9 | 160 | 25.2 | 1218 |
| 50 | SBS wk 2 01 | 0.081 | 71 | S 59 At 24 PI 11 BI 05 Ep 01 | 68 | 18.7 | 245 | 38.5 | 2136 |
| 51 | SBS wk 2 01 | 0.101 | 71 | S 45 Ep 26 At 24 BI 05 | 79 | 18.8 | 294 | 40.6 | 1287 |
| 52 | SBS wk 2 03 | 0.101 | 71 | S 46 At 32 PI 22 | 69 | 19.4 | 236 | 38.1 | 2139 |

Appendix 2

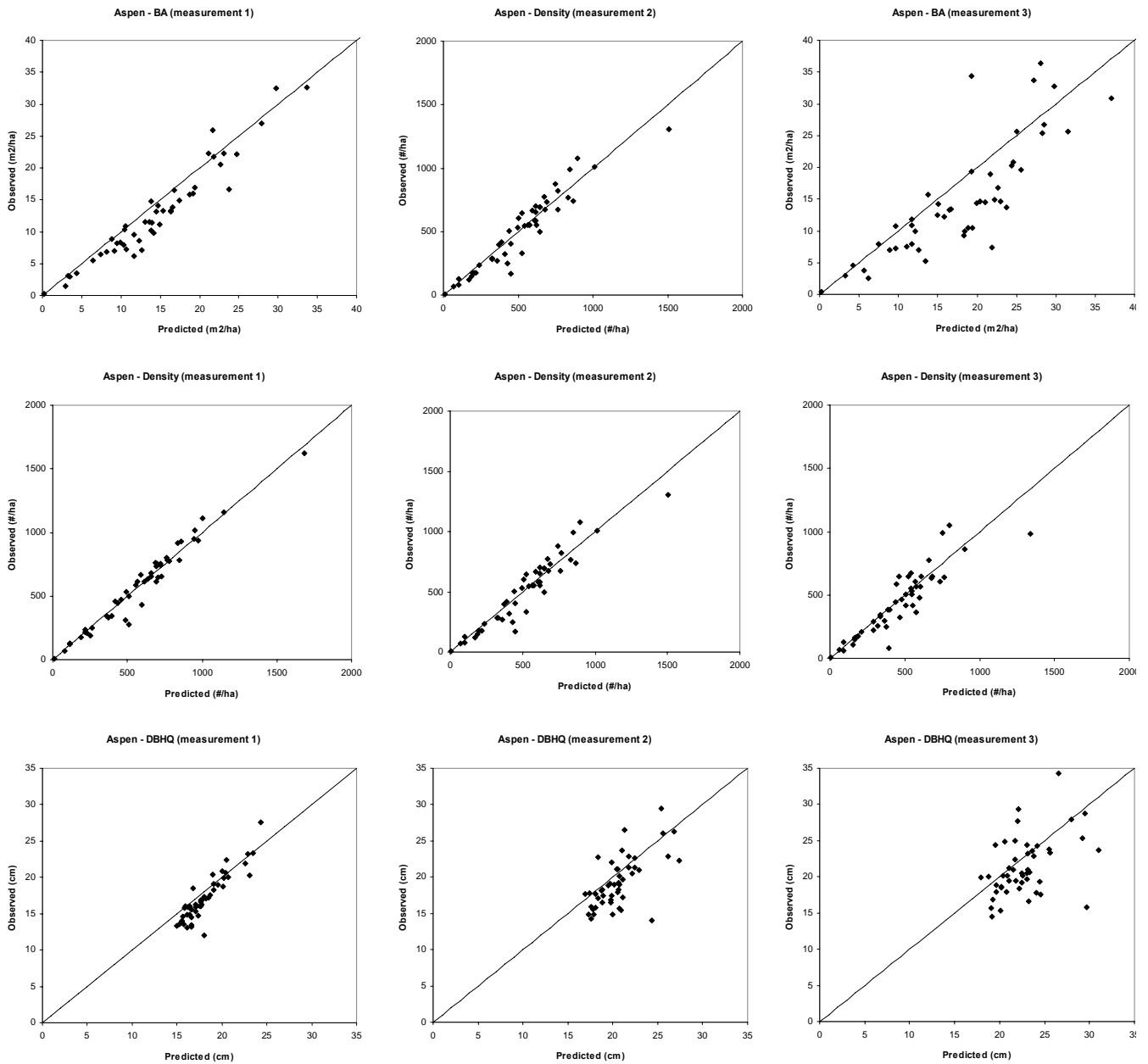


Figure 1: 1:1 plots for aspen. Observed basal area (BA, m^2/ha), density ($\#/ha$) and quadratic mean diameter (DBHQ, cm) for aspen are compared to predicted value from SORTIE-ND simulations of 51 permanent sample plot from the SBS zone in British Columbia. The permanent sample plots are described in appendix 1 and are located in uneven-aged mixed species stands containing aspen, lodgepole pine, hybrid spruce and subalpine fir.

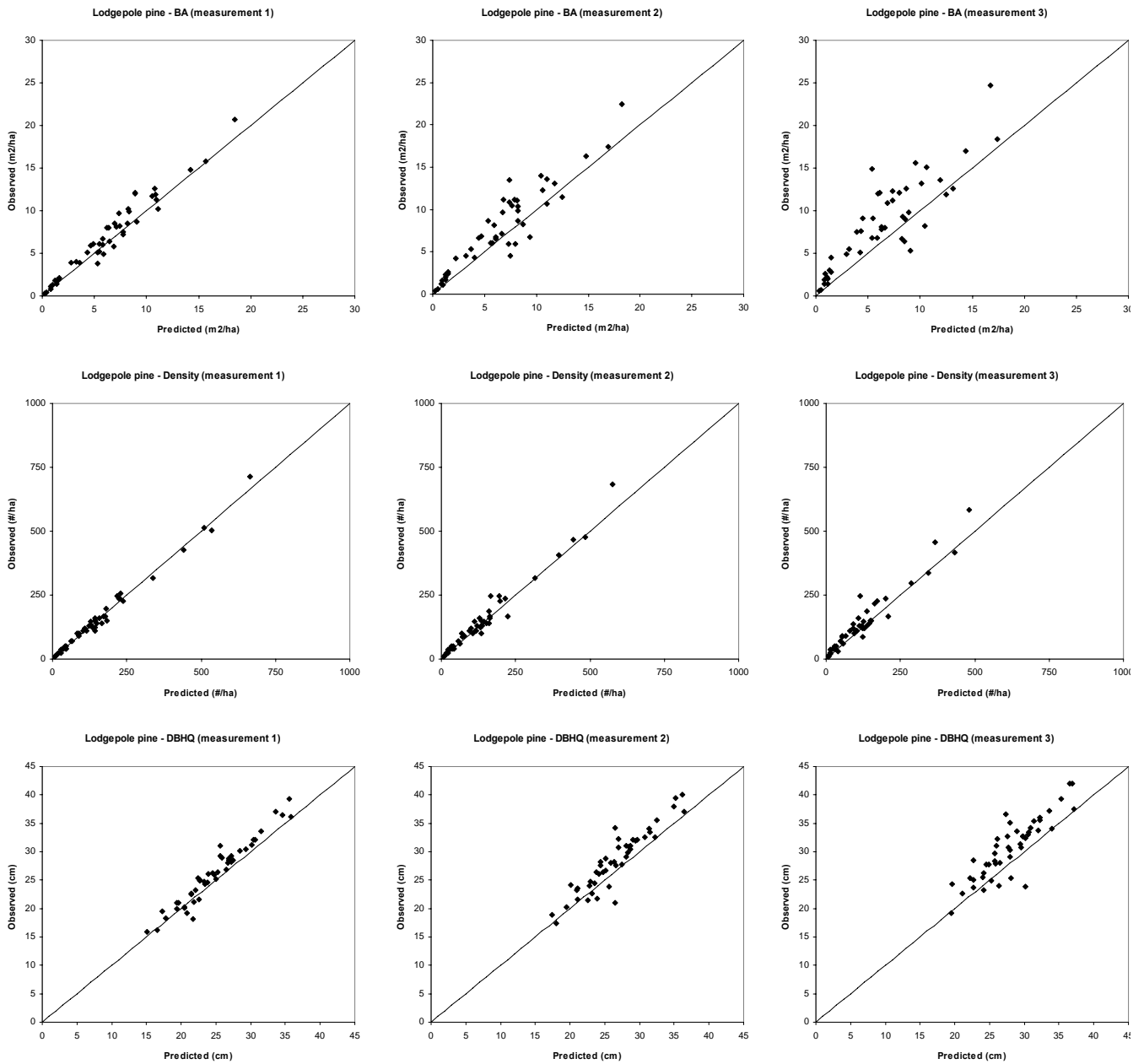


Figure 2: 1:1 plots for lodgepole pine. Observed basal area (BA, m²/ha), density (#/ha) and quadratic mean diameter (DBHQ, cm) for lodgepole pine are compared to predicted value from SORTIE-ND simulations of 51 permanent sample plot from the SBS zone in British Columbia. The permanent sample plots are described in appendix 1 and are located in uneven-aged mixed species stands containing aspen, lodgepole pine, hybrid spruce and subalpine fir.

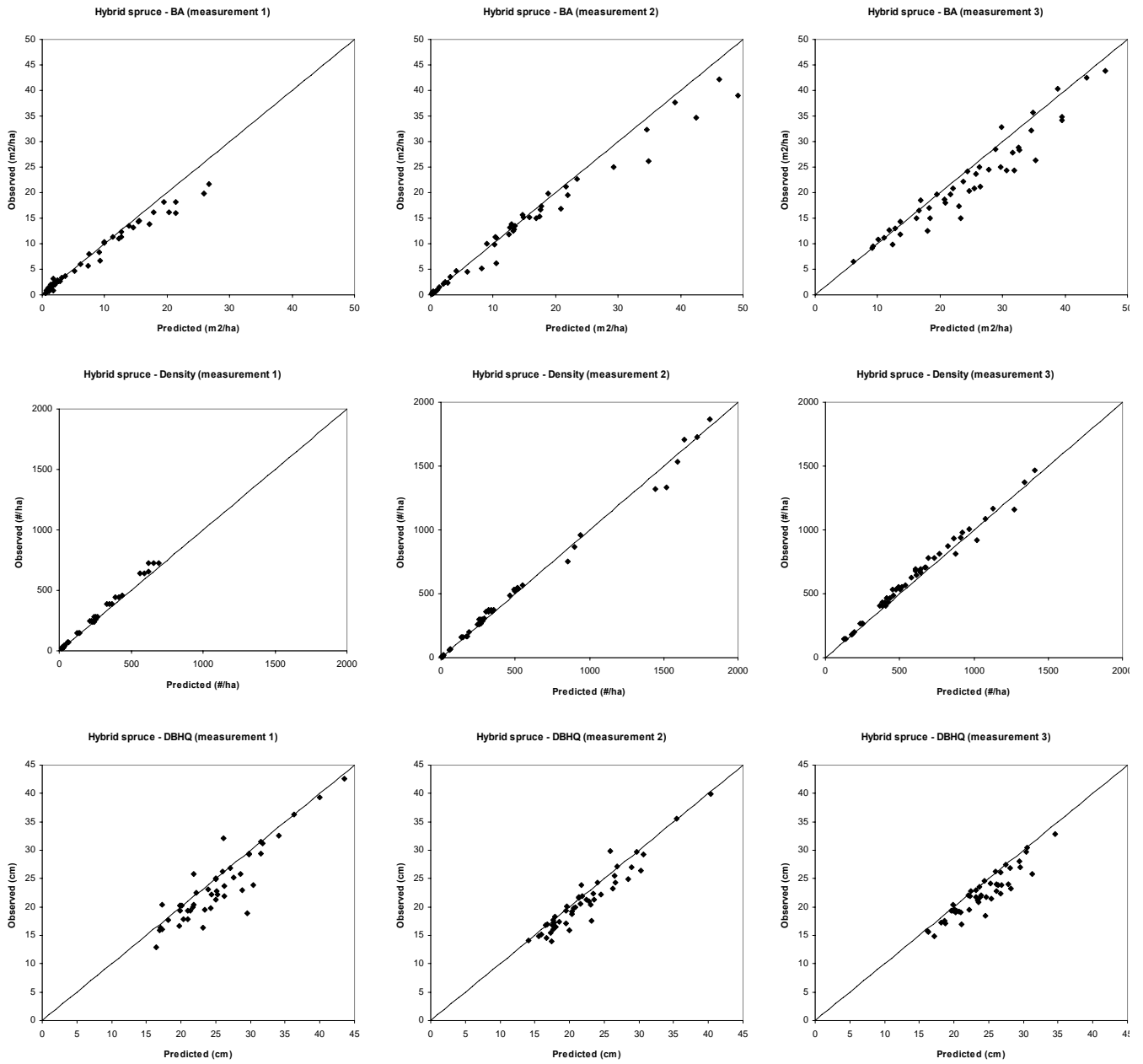


Figure 3: 1:1 plots for hybrid spruce. Observed basal area (BA, m²/ha), density (#/ha) and quadratic mean diameter (DBHQ, cm) for hybrid spruce are compared to predicted value from SORTIE-ND simulations of 51 permanent sample plot from the SBS zone in British Columbia. The permanent sample plots are described in appendix 1 and are located in uneven-aged mixed species stands containing aspen, lodgepole pine, hybrid spruce and subalpine fir.

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