Modeling stand dynamics in Scots pine (Pinus sylvestris L.) forests of the Southwestern Alps

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MODELING STAND DYNAMICS IN SCOTS PINE (*PINUS SYLVESTRIS* L.) FORESTS OF THE SOUTHWESTERN ALPS

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Se i pini erano indorati dal sole,
se i ruscelli cadevano nelle loro cascatelle luccicando,
se le margherite e gli altri fiori ed il cielo erano in festa per l’estate,
più forte era la visione d’un sole…

…E faceva sì che esse non fossero così come noi le vediamo,
ma tutte, per così dire, l’una dell’altra innamorate.
Per cui, se il ruscello finiva nel lago,
se un pino s’ergeva accanto ad un altro pino, era per amore.

A Rosina.

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Abstract

Scots pine (*Pinus sylvestris* L.) forests cover more than 28 millions hectares in Europe, i.e., about 20% of total forest cover. In the Western Alps, Scots pine stands (31,000 ha) grow both in the outer and in the inner, continental sectors, on elevations ranging from the Po plain to the upper mountain belt.

Current stand structure in the Alpine regions has been shaped by anthropogenic influence for the last centuries, This is especially true for pine forests, that show greater sensitivity to land use and environmental changes due to their vast distribution and their early-seral character. Besides the ongoing and ubiquitous land abandonment pattern, a novel phenomenon has appeared in the last decades, namely a dieback wave which is undermining the continuity of the services supplied by the pine forests.

For this reasons, sustainable forest management of pine stands must be the subject of scrupulous consideration. The peculiar climatic and site conditions in the Alps and the close interaction between forest dynamics and human activities suggest the need for a more thorough understanding of ongoing processes. A deeper knowledge may represent the basis for designing prediction models of stand structure and dynamics to support silvicultural management.

We identified competition as the main process driving tree and stand development. The present research focuses on the analysis of competitive and mortality dynamics on different spatial and temporal extents (from tree to stand and district). The aims of the present work are: (a) to describe current distribution of Scots pine in the Southwestern Alps, with a special focus on region-wide changes in land use and climate regimes and their potential effect; (b) to design a silvicultural decision support tool, capable of predicting stand development on a regional scale and comparing management alternatives for the pursuit of the desired silvicultural goals; (c) to analyze the mode of intra- and interspecific competition in Scots pine stands and to assess its effects on both individual growth and on tree survival as an emergent property, also

including interactions with land use history; (d) to test the applicability of an individual-based growth and yield model to local species and growing conditions, foreseeing its implementation for the analyzed stands.

The methods of this research are aimed at the reconstruction of past stand history, at the understanding of present dynamics and at modeling future stand structure and composition. For this reason we integrated available forest inventory data with dendroecological measurements from a new permanent network of sample plots, located in the main pine cover types of the study area. The development of the research is based on a gradual refinement of the scale of investigation, ranging from historical landscape analysis to region-wide fitted biometric relationships, to local competition analysis by means of numerical indices and geostatistical techniques, to the modelling of individual tree growth and mortality. Our results show that Scots pine is characterized by a rapid response to environmental and land use change. The species has a great potential for colonization, and can originate a massive and homogeneous establishment where climate is not limiting and land abandonment was more pronounced. Most of the younger stands show quick and well-defined dynamics, drived by competition for light in the earlier self-thinning stage and by structural differentiation in the reinitiation phase or leading to succession of late-seral species in mature stands. On the other hand, where site fertility is limiting and disturbances play a negative impact on pine growth and survival, dynamics are slower. Here, competition may be locally intense but is not the main population regulatory factor. In all cases, land use history has been shown as having a stronf influence on ongoing competitive dynamics and their consequences at the stand level, i.e., the survival-mortality equilibrium.

In the last chapter a calibration and sensitivity test of US Forest Service’s individual-base growth model, the Forest Vegetation Simulator, is shown. FVS was validated on local inventory data for the Fort Bragg NC forest area, characterized by a vast extension of Longleaf pine (*Pinus palustris* Mill.) constituting the main habitat for the endangered red-cockaded woodpecker

(*Picoides borealis*). Available growth projections are hampered by a general overprediction of density and yield, as compared to both field-based evidence and the biological constraints of the species. Successful calibration of the many growth submodels of FVS, carried out based on more than 140,000 tree measurements (11,000 sample plots, years 2002-2003 inventory), enabled managers to rely on more accurate growth predictions. Flexibility to user input is among the desired features of a species-wide prediction model for Scots pine dynamics. Deconstruction, calibration and testing of an existing forest growth and yield model over localized inventory data provided the basis to propose data and research needs for implementing such framework in Alpine forests.

Last, the design and implementation of a Density Management Diagram proved useful to project, visualize and compare silvicultural goals and management strategies aimed at their pursuit. The diagram is based upon the self-thinning law. It was designed using region-wide forest inventory data, and field-based data from permanent plots as a control and validation dataset. By characterizing silvicultural goals in terms of quantitative stand parameters, we devised different scenarios according to the functions whose supply is demanded to the pine forest, and effectively compared the trajectories of stand development associated to alternative management strategies. We also tested implementation on the diagram of natural disturbance regimes, which we reconstructed from historical and field evidence, in order to forecast the most likely stand response.

The combined analysis of different spatio-temporal scales, i.e., region-wide forest inventories and intensive plot measurements, allowed us to model inferred dynamics across a wide range of organization levels in the community, from trees to whole landscapes. The establishment of a permanent monitoring network will prove its utility with upcoming repeated measurements. The natural prosecution of this study will be the design of a inventory network suitable for constructing a local variant of the described model, and the statistical implementation of such tool in mountain forests of the Alps over a wider range of key species.

Riassunto

Il pino silvestre (*Pinus sylvestris* L.) occupa in Europa una superficie di oltre 28 milioni di ettari, pari al 20% delle foreste del continente. Nelle Alpi occidentali, i popolamenti di pino silvestre (31 000 ha) occupano tutte le zone bioclimatiche, da quella esalpica alle parti più continentali delle valli interne, in una fascia altitudinale compresa tra la pianura padana e il piano montano superiore.

L'attuale struttura dei popolamenti delle regioni alpine è il risultato dell'influenza che negli ultimi secoli l'uomo ha esercitato sull'ecosistema forestale; questo vale in modo particolare per le pinete, più sensibili all'impatto antropico a causa delle loro distribuzione e della loro autoecologia. Il carattere pioniero della specie la rende infatti capaci di rispondere rapidamente ai mutamenti ambientali e ai disturbi di origine naturale o antropica. Ai disturbi di lunga durata si sono aggiunti nell'ultimo secolo gli effetti dell'abbandono dei territori montani verificatosi a partire dall'ultimo dopoguerra, in seguito al quale è aumentata la superficie di ex-coltivi ed ex-pascoli disponibili alla colonizzazione di specie forestali a carattere pioniero. Dall'altro lato, le foreste di pino silvestre delle vallate interne subiscono da diversi anni evidenti processi di deperimento, in particolar modo nelle aree più siccitose. Tali cambiamenti possono esercitare i loro effetti a livello di popolamento, di comunità e di paesaggio, e ripercuotersi sull'equilibrio uomo-foresta ponendo nuovi rischi per la stabilità e la continuità dei servizi prestati dai popolamenti.

Per questi motivi, la gestione selvicolturale delle pinete deve essere oggi soggetta ad una particolare attenzione. Le condizioni climatiche ed ecologiche delle Alpi occidentali, e la stretta interazione che vi ha luogo tra le attività antropiche e le dinamiche forestali, suggeriscono la necessità di indagare a fondo le dinamiche in atto, e di elaborare strumenti di previsione della struttura e composizione futura dei popolamenti, utilizzabili a supporto alla gestione selvicolturale. A tale scopo, il processo di competizione intra- ed interspecifica nei popolamenti forestali è stato identificato come la dinamicha-chiave nel

determinare lo sviluppo futuro dei popolamenti. Le dinamiche di competizione e mortalità nelle pinete delle vallate alpine sono state analizzate secondo un approccio multiscalare, concentrando l'analisi su differenti risoluzioni spaziali (regionale, di popolamento e locale) e temporali.

Gli obiettivi della ricerca sono: (a) Analizzare la distribuzione attuale del pino silvestre nelle Alpi sudoccidentali, descrivere le tipologie forestali e le comunità cui esso partecipa, esaminare i cambiamenti avvenuti negli ultimi decenni a scala regionale ponendoli in relazione con l'uso del territorio da parte dell'uomo; (b) Predisporre un sistema di supporto alle decisioni selvicolturali a scala regionale, capace di prevedere lo sviluppo dei popolamenti in funzione della struttura attuale e di descrivere differenti obiettivi di gestione prefigurando la strategia selvicolturale per perseguirli, anche in presenza di scenari di cambiamento delle condizioni future; (c) Esaminare l'influenza esercitata dalla competizione intra- e interspecifica sugli accrescimenti e sulla mortalità individuale ed analizzare l'effetto della storia dei popolamenti e dell'uso del suolo su tali dinamiche; (d) Testare un modello di previsione di accrescimento a scala individuale che possa successivamente essere applicato ai popolamenti analizzati.

I metodi utilizzati per la presente ricerca, finalizzati alla ricostruzione della storia dei popolamenti, allo studio delle dinamiche in corso e alla modellizzazione di quelle future, hanno previsto l'integrazione di dati di inventario a scala regionale con rilievi dendroecologici effettuati in aree di monitoraggio permanenti, distribuite nelle principali tipologie forestali proprie del pino silvestre in Piemonte e Valle d'Aosta. Le diverse fasi dello studio sono caratterizzate da un progressivo affinamento della scala spazio-temporale di analisi: dall'esame di foto aeree per l'analisi dei cambiamenti di uso del suolo negli ultimi 50 anni in paesaggi dominati dalle pinete, alle procedure di statistica inferenziale utilizzate per calibrare relazioni allometriche tra i parametri descrittivi dei popolamenti su scala regionale, all'analisi della competizione su scala locale (di popolamento) mediante indici sintetici e tecniche di geostatistica, alla modellizzazione della crescita e della mortalità dei singoli alberi nel contesto di un software di modellizzazione individuale.

I principali risultati confermano che il pino silvestre è una specie caratterizzata da una risposta rapida ai cambiamenti ambientali e di uso del suolo. La specie, dotata di un grande potenziale di insediamento, è stata la componente principale di un'afforestazione massiva e uniforme laddove il clima era più favorevole e l'abbandono da parte dell'uomo più accentuato. Gran parte dei popolamenti più giovani mostra una dinamica rapida e ben definita, guidata dalla competizione per la luce nelle fasi di autodiradamento e dalla differenziazione strutturale che prelude alla fase di rinnovazione o alla successione con specie definitive nei popolamenti più maturi. A tale situazione fanno da contrasto i popolamenti a condizionamento edafico o caratterizzati da una intenso impatto dei disturbi. Qui le dinamiche sono rallentate, la competizione può essere localmente intensa ma non rappresenta il principale fattore di regolazione delle popolazioni. In particolare, l'impatto antropico ha dimostrato di essere assai influente nel determinare i rapporti compatitivi in atto e l'intensità del processo di autodiradamento che rappresenta l'esito di questi al livello gerarchico superiore. L'uso di metodologie di analisi indipendenti, integrando l'analisi dell'evidenza in campo con la consultazione di archivi storci e, grazie a metodi dendrocronologici, biologici, si è rivelato utile alla ricostruzione della storia di ciascun popolamento in esame e alla formulazione di ipotesi e modelli di previsione circa il suo futuro sviluppo.

Il modello di crescita forestale Forest Vegetation Simulator è stato sottoposto ad un test di applicabilità, effettuandone la validazione sulla base di dati inventariali. Il caso di studio è rappresentato dal comprensorio di Fort Bragg, North Carolina, caratterizzato da estesi popolamenti di *Pinus palustris* che rappresentano l'habitat principale di *Picoides borealis*, una specie segnalata a rischio di estinzione. Le proiezioni di accrescimento attualmente disponibili sono limitate da una generale sovrastima degli accrescimenti e della biomassa, sia rispetto ai dati di inventario che nei confronti dei limiti biologici delle specie analizzate. La calibrazione e validazione dei modelli di crescita che compongono il programma, utilizzando come dataset di riferimento le misure realizzate in situ negli anni 2002-2003 (140.000 alberi, 11.000 aree di saggio), hanno consentito di disporre di proiezioni più accurate e realizzate su misure a scala locale. La flessibiltà del Forest Vegetation Simulator nel rappresentare specie e condizioni stazionali localizzate è una caratteristica chiave per l'elaborazione di un modello di previsione delle pinete alpine basato sulle dinamiche studiate effettuate a scala individuale.

Infine, la calibrazione di un diagramma per la gestione della densità si è dimostrata utile alla programmazione, visualizzazione e valutazione degli obiettivi selvicolturali e delle alternative gestionali necessarie a perseguirli. Il diagramma, basato sul principio dell'autodiradamento, è stato elaborato utilizzando dati provenienti dall'inventario forestale regionale e, come dataset di supporto e validazione, le misure effettuate nelle aree di studio insediate nel corso della ricerca. A seconda delle funzioni richieste alla pineta sono stati ipotizzati scenari differenti, caratterizzando gli obiettivi selvicolturali con parametri strutturali quantitativi e valutando le alternative gestionali atte a raggiungerli. Si è inoltre testata la possibilità di utilizzare il diagramma per valutare la risposta dei popolamenti ai disturbi naturali, ricostruendo i regimi di disturbo grazie ai dati biologici e storici a disposizione.

L'integrazione di metodi di analisi multiscalari ha consentito di modellizare le dinamiche in atto nelle pinete alpine a diverse risoluzioni spaziali e temporali, dalla competizione tra individui alla previsione della struttura e composizione dei popolamenti a medio e lungo termine. L'insediamento di una rete di aree di monitoraggio permanente si dimostrerà utile quando saranno disponibili le prime ripetizioni delle misure effettuate. La presente ricerca rappresenta la base di conoscenza necessaria alla progettazione di una variante localizzata dei modelli di crescita sperimentati e alla loro applicazione alle principali tipologie forestali dell'area alpina.

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Chapter I: Introduction

Scots pine (*Pinus sylvestris* L.) is the most widespread conifer in the world (Nikolov and Helmisaari, 1992) and hence in Europe [Figure 1], where it covers more than 28 million hectares (20% of total forested area) (Mason and Alía, 2000). Natural forests or plantations of this species are found in all member states of the EU on a variety of soils and in extremely diverse climates, from oceanic to continental, and from alpine to Mediterranean (Ellenberg, 1988; Médail, 2001).

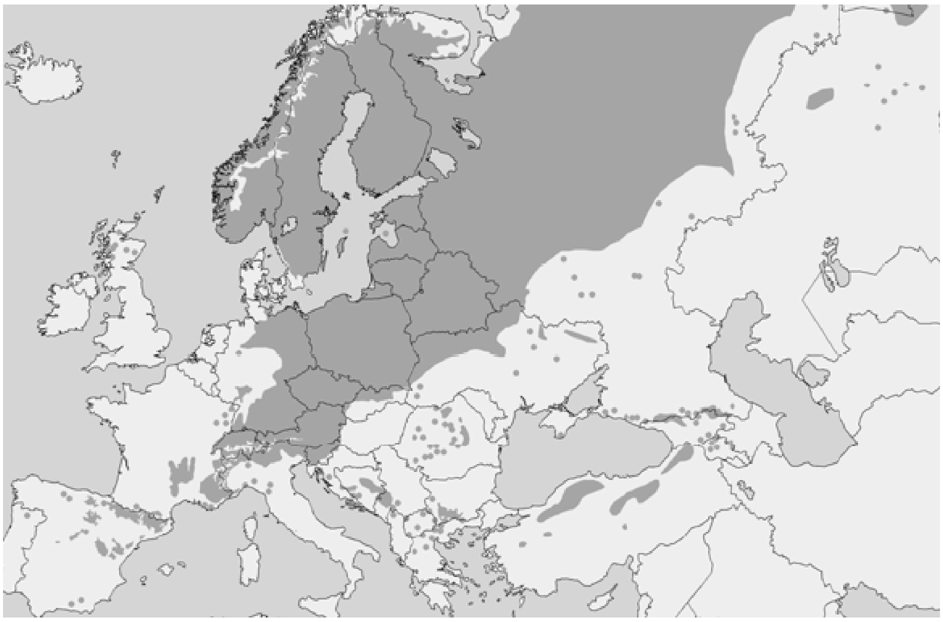


Figure 1 – Range of Pinus sylvestris *L. in Europe (from Csaba et al., 2003). The range spreads over a distance of 14,000 km, from 8ºW in Spain to 141ºE in Russia and from latitude 70ºN to 37ºN (Boratynski, 1991).*

As a consequence, the species is differentiated into many varieties or ecotypes (Białobok, 1970). On grounds of habitat and flora, Ellenberg (1988) summarized the *Pinus sylvestris*-dominated communities in Central Europe in seven groups. The first four were grouped together as “southern” or “species diverse” pinewoods, whilst the other three were classed as “northern”, “species poor” or “acid-humus” pinewoods. Rodwell and Cooper (1995) also produced a summary of the *Pinus sylvestris*-dominated communities in Europe. A recent overview of the phytosociological classification of European plant communities in which *Pinus sylvestris* is a significant component was presented by Kelly and Connolly (2000).

Scots pine is a light demanding, usually early seral species that can establish both in acid and limestone soils (Richardson, 1998; Debain et al., 2003). Its ecology is largely characterized by stress tolerance. On the one hand this allows it to occupy a range of habitats that are unfavorable to other tree species, through tolerating various combinations of climatic and edaphic stress, including low temperatures, extremes of acidity and alkalinity, extremes of waterlogging and of drought (Richardson, 1998). On the other hand, this implies that Scots pine is excluded from more favorable sites through competition.

Pine forests fulfill very different roles in the various European countries, ranging from pioneer communities established on abandoned agricultural land in parts of western and central Europe (Caplat et al., 2006) to a natural forest in parts of Scandinavia and in the mountains of north-central Spain (Mason and Alía, 2000).

The present study is focused on two mountain regions in north-western Italy. In the western Alps Scots pine has a wide altitudinal range (from the Po plain at 100 m a.s.l to the valleys up to 2000 m a.s.l.) and climatic distribution, encompassing both the external Alps with an average annual rainfall of more than 2000 mm and the internal, continental valleys with an average annual rainfall ranging between 500 and 600 mm (Richardson, 1998). In the Po plain it was introduced more than 200 years ago and now is more or less naturalized as a pioneer species in the coarse-textured soils, where it can be very competitive. In the external-intermediate sectors of alpine valleys it is usually a pioneer species that has been favored by past fires (Gobet et al., 2003), heavy forest cuts, and by the recent increase of fallow lands (Farrell et al., 2000; Krauchi et al., 2000; Caplat et al., 2006). Here, pine-dominated vegetation due to rapid recruitment (Picon-Cochard et al., 2006) is usually an intermediate step in succession to a late-seral stage dominated by broadleaved trees (or mixed broadleaved-coniferous forest at higher altitudes), at least where a lack of disturbance or suitably favorable conditions permit shade-tolerant species to be strong competitors. The internal (continental) sectors of the alpine valleys are the only sites where Scots pine could be considered stable (Ozenda, 1985). In this environment this pine is both the early-seral and late-seral species because in these dry condition (less than 700 mm year^{-1} rainfall) it is a strong competitor with respect to the other conifers.

Stands present a wide range of age, structure and composition. Depending on climatic and morphological factors, pine stands may be almost 100% pure (especially on dry, southern slopes). When yearly precipitations provide higher moisture rates in the soil, or after the initial phase of pioneering colonization on former meadows, species mixture is the rule, since competitive strength of Scots pine tends to fade out. Common mixes occur with Swiss mountain pine (*Pinus montana* Mill.), European larch (*Larix decidua* Mill.), Norway spruce (*Picea excelsa* Karst.), Silver fir (*Abies alba* Mill.), Beech (*Fagus sylvatica* L.), Sessile oak (*Quercus petraea* (Mattus.) Liebl), European chestnut (*Castanea sativa* Mill.), and most often with Downy oak (*Quercus pubescens* Willd.) which has similar thermal and moisture needs. Pine-Downy oak mixed stands are usually xerophitic communities, remnant of old oak stands where pine was favored by intense logging, or either former pure mature pine stands where regeneration of mid-tolerant species is more likely due to natural succession and land use changes. In any case, the broadleaved component indicates a more advanced successional stage and shifting towards a late-seral community. Variants of pine cover type with birch or other early-serals are common in secondary colonization of abandoned fields, on rocky sites and as post-disturbance community (IPLA, 1996).

According to the last regional forest inventories (IPLA, 2003a, 2004) pure Scots pine stands in the study area occur on 32.000 ha (3.5% of total forest land cover). Most pine forests occupy the more continental, inner sectors of alpine valleys; relic stands can be found on former peatlands in the northeastern lake district [Figure 2].

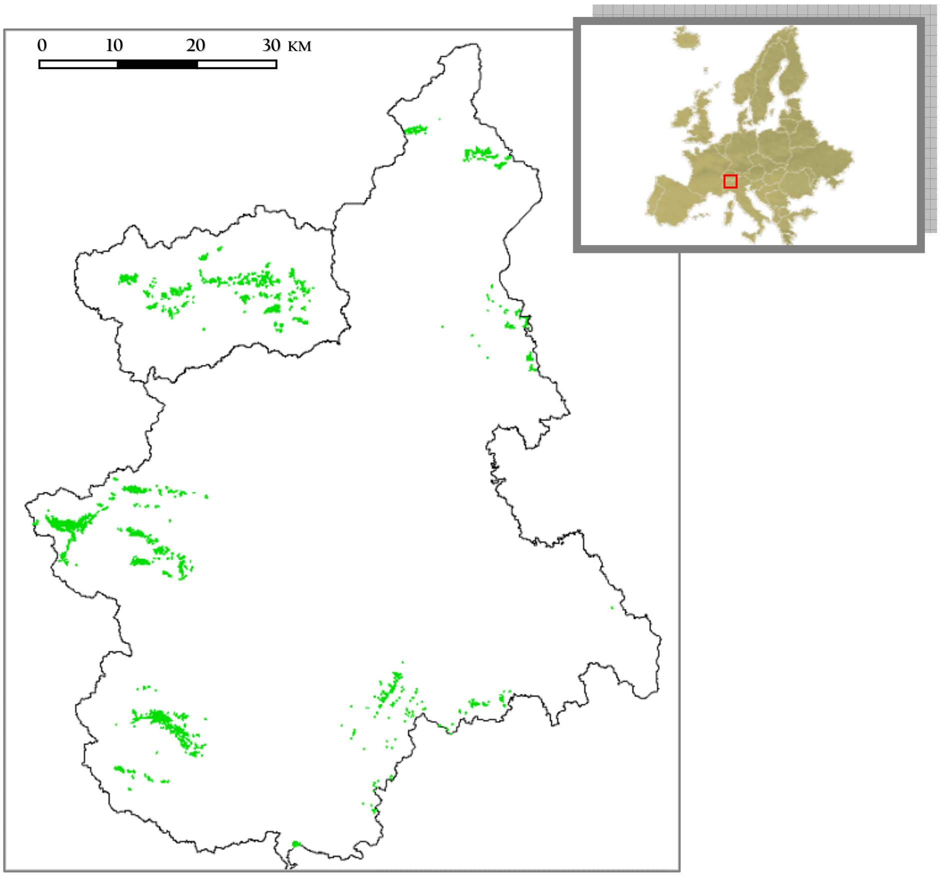


Figure 2 – Distribution of pure Scots pine stand in the study area.

Problem statement

In the last decades, European forest management has been characterized by a shift from traditional production forestry to a multifunctional strategy (Attiwill, 1994; Führer, 2000; Brang et al., 2002; Harvey et al., 2002). As stated by the Ministerial Conferences on Protection of Forests in Europe held in Strasbourg (1990), Helsinki (1993) and Lisboa (1998), sustainable forest management calls for balancing diverse ecological, social, and economic values over space and time (Sheppard and Meitner, 2005). Therefore, it must rely upon a multifunctional approach in order to provide adequate answer to the society demands, i.e., conservation and increase of biodiversity, recreational and tourism use, environmental buffering of climate changes, and soil conservation concerns (Peng, 2000; Varma et al., 2000).

The extent of the resource, and its potential value in both financial and non-market terms, indicates that Scots pine forests can provide a major contribution to the economic, environmental and social development of the EU's rural economy in the twenty-first century. The challenge is to develop management systems appropriate to region and site that can provide varied forests to meet productive, social and environmental requirements (Mason, 2000) [Figure 3].

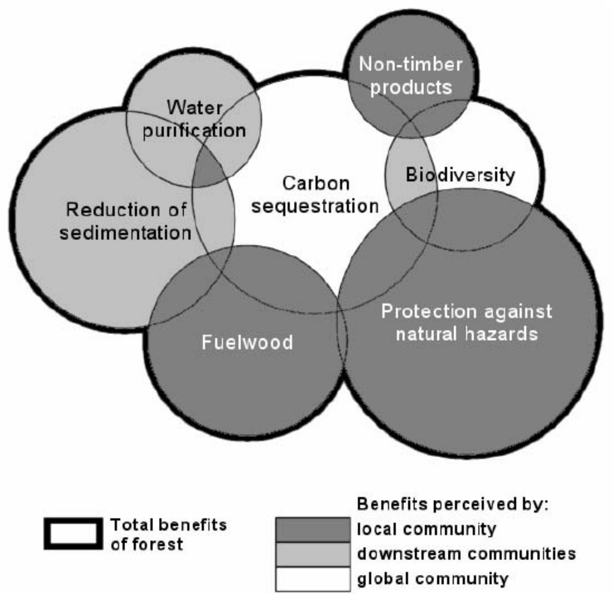


Figure 3 – Benefits and beneficiaries of mountain forest services (from Pagiola et al., 2002).

The wide tolerance of Scots pine to site and climatic conditions has meant that stands of this species have been managed using a range of silvicultural practices. Since Scots pine is a light-demanding species, the forests tend to have comparatively simple and regular stand structures. Because of the importance of the species in various European countries, at a national level there is appreciable knowledge about the effect of silvicultural regimes, the amount of genetic variation in different populations, and about characteristic flora and fauna of the pinewood ecosystem (Mason and Humphrey, 1999).

However, many of the silvicultural models devised in the century-long history of forest science in Europe are no longer applicable to the current conditions in the Alps, not only for the undue emphasis given by traditional forestry to timber production goals (Bengston, 1994), but also because of the peculiarities of mountain forests as compared to the ecosystems of central and northern Europe.

Mountain forest management and forest utilization differ from management schemes applied elsewhere mainly with respect to the long temporal sequences of vegetative succession, the remoteness of the forests and their limited accessibility (Brang et al., 2002). Due to their high altitude, steep slopes and harsh climate, but also because of the location of settlements and communication systems underneath, these forests, although frequently very important for timber production, also play an important role for soil conservation and for the control of the water regime. Therefore, many forests simultaneously provide timber, recreation, protection, nature and water conservation, fungi, berries and animals for hunting. With increasing population density and pressure from emerging tourism in the Alpine environment, the demand for hydrological, environmental (e.g., wildlife habitat) and recreational services from mid-elevation Scots pine forests has been continuously increasing.

Recent changes in pine forest cover

The actual structure of mountain forests in the Mediterranean region has been shaped by anthropogenic activities for centuries (Uggla, 1974; Pons and Quézel, 1985; Vernet, 1997; Blondel and Aronson, 1999); this is true especially for pine forests, due to the silvics of the species and to the wide home range it occupies (from the plains to mid-elevation slopes, i.e., the areas most impacted by human presence).

In the last 7,500 years, forested area held by late-seral communities has significantly shrunk, due to forest and agricultural land use change, selective logging, firewood and litter collection, and grazing (Farrell et al., 2000; Krauchi et al., 2000; Saponeri, 2006). After centuries of heavy human influence, in a large part of the present stands the succession from Scots pine to more tolerant broadleaves and conifers is very slow.

Nonetheless, this trend has all but persisted in the last decades. The chronic disturbances caused to mountain forest ecosystems by human activities have been replaced by massive land abandonment since World War II (Antrop, 2004). Unfavorable topography, low accessibility and poor incomes were identified as the most relevant causes (Walther, 1984; Bebi and Baur, 2002); the abandonment of rural areas has been leading to a strong polarization between accessible urbanized areas and underdeveloped rural land (Antrop, 2004). Abandoned farmland is undergoing a process of colonization by tree and shrub species (Surber et al., 1973; Roche et al., 1998; Garbarino and Pividori, 2006); large areas formerly occupied by meadows and pastures were made available for colonization by early-seral forest species (Naveh, 1993; Poyatos et al., 2003). As a consequence, a new landscape, predominantly covered by forest, is currently taking the place of the former pastures-meadows-forests mosaic. The speed of forest expansion varies across multiple gradients of physiographic attributes, regional climate factors and land use history, i.e., time since the land was last cultivated or grazed (Bebi and Baur, 2002; Poyatos et al., 2003;

Chauchard et al., submitted). This trend is observable both in Mediterranean (Baudry, 1991) and temperate areas (Poschlod et al., 2005) of Europe.

Because of its wide range, its strong early-seral character, i.e., reacting quickly to land-use change, and thanks to its strong dependence on humans for persistence (Higgins and Richardson, 1998), Scots pine responds quickly to changes taking place in the landscape over relatively short periods. The recent area increase of abandoned fields and grasslands and the modification of fires regimes resulted in vegetation types where pine germination could easily occur (Naveh, 1993). As a result, the frequency of Scots pine increased and, today, pine forests extend well beyond what their natural range would encompass in the absence of recent disturbances (Plumettaz Clot, 1988; Barbéro et al., 1990).

An increase in forest area occupied by pine has been witnessed during the twentieth century in most European regions. A study aimed at describing the effect of land use change on the spatio-temporal dynamics of pine-dominated forest landscape in western Alps over the last 50 years evidenced an average increase by 30% of forest cover [Figure 4]. This process was characterized by different patterns, which varied with initial landscape fragmentation, elevation and aspect, and socio-economic variables promoting or not a prolonged human presence on the sites (Garbarino at el., 2006). However, Scots pine consistently showed rapid response to land use changes, adopting a double-sided colonization strategy that consisted either in a massive and rapid invasion, or in a more fragmented and episodic colonization to adapt to the spatial arrangement of the areas released from anthropogenic influence (Vacchiano et al., 2006a; but see Caplat et al., 2006 for an alternative model).

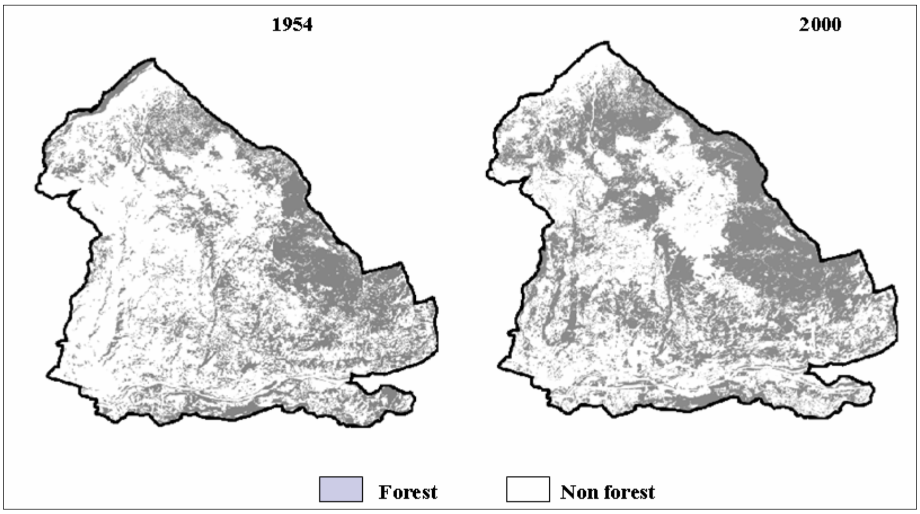


Figure 4 – Pattern of 50-years afforestation on a pine-dominated slope in northern Italy (surface area: 3,500 ha).

The implications of such a new landscape pattern reach far into ecosystem processes and management options, influencing the stability and resilience of the ecosystem (Farrell et al., 2000), the intensity and rate of spread of disturbances (Turner, 1989) such as fire or parasitic and pathogenic attacks, the extent and quality of wildlife habitats, the amount and persistence of plant and animal biodiversity, the intensity and direction of matter and energy flows, the opportunities for timber and other commercial forest products. Vast even-aged, monospecific areas have a low structural diversity and are considered hazardous for stand stability due to higher proneness to fire, pest and insect outbreaks and other disturbance agents (e.g., Gardiner et al., 2005).

In some instances, the described trend was stabilized, or even reversed, in the latter decades of the last century. Given enough time, the reduction in management intensity ultimately facilitates the succession of stands composed of early seral species (Piussi and Farrell, 2000). Pure pine stands are increasingly being replaced by more complex structures (mixed or broadleaved forests); the proportion of mixed stands of Scots pine and a range of other species is soon expected to rise (Mason and Alía, 2000).

New hazards to stability of pine forests in the Alps

These dynamics are further reinforced by recent large-scale processes that could severely change the species' distribution and its potential use as a resource to exploit. The functioning of mountain forest ecosystems, i.e. their ability to sustainably secure societal needs, is at risk under changing climatic conditions. The distribution of vegetation types can be treated as determined by the interaction of temperature and water regimes (Ellemberg, 1988; Holdridge 1964; Ozenda, 1985); temperature-limited ecosystems such as the ones in high mountains are thought to be very sensitive to greenhouse warming (Markham et al., 1993). The component of climate change on which most attention has been focused is increasing temperature, which would in turn result in other changes (e.g., soil moisture, evapotranspiration, fire regimes) which are not easily predicted (Price and Haslett, 1995; Ciais et al., 2005). Changes in precipitation or temperature regimes can influence several development stages in *Pinus*: seed production, germination, emergence, seedling mortality and growth (Despland and Houle, 1997).

The ability of tree species to maintain viable and persistent populations under changing climate regimes could be affected by numerous interactions between populations dynamics, stochastic events and micro-site features (Chen et al., 1992; Halpin, 1994). Most transient changes in the structure of forests, such as the decline of certain tree species, are driven by a combination of climatic and anthropogenic changes and are modified by local, biological interactions acting on temporal scales ranging from months to centuries (Spies, 1998).

For instance, the distribution of forest species could be significantly changed as a result of altered fire frequencies, as has happened as a result human actions (Daubenmire, 1943). The frequency of fires in many mountain ecosystems has been modified considerably by human actions, further complicating the projection of species' distribution under new climates. Since photosynthesis is often limited by current temperature and CO_2 concentration, one can hypothesize that increases in these variables will lead to increased growth of vegetation and therefore to increased fuel loading. This problem could be exacerbated if mortality increases because trees are living in less optimal conditions and, particularly, if evapotranspiration increases (Franklin et al., 1992).

Unusually high mortality of Scots pine has recently been observed in many inner-alpine valleys (Müller-Edzards et al., 1997; Cech and Perny, 1998; Vertui and Tagliaferro, 1998). On the northern side of the Alps, up to half of the pines reportedly died between 1995 and 2000 (Dobbertin et al., 2005). On the Italian side, Scots pine has almost disappeared from mixed forests of middle-low altitude on north-facing slopes; the mortality was later recorded also on the lower belt of the South-facing slopes. At higher altitudes the forests were almost free of dieback (Vertui and Tagliaferro, 1998).

Two different types of mortality were evident: sudden death of previously healthy individuals, usually in springtime, or a progressive and long decay, characterized by thinning out of the crown, death of small branches and sometimes of the tree top, and eventually leading the tree to death. With loss of needles, the tree has reduced ability to produce the energy it needs to survive: reduced shoot growth (shortened internodes) is common on trees experiencing decline. The phenomenon affects singles trees and small groups, and both mature and young individuals.

These high mortality rates are causing considerable concern about the long-term sustainability of the Scots pine forests in the Alps. The exact causes of the present mortality episode have not been established and are currently under investigation (Dobbertin, 1999; Rigling et al., 1999; Rigling and Cherubini, 1999; Rebetez and Dobbertin, 2004; Rigling et al., 2004; Bigler et al., 2006; Rigling et al., 2006). Known agents of decay did not appear to be the main cause of mortality. Commonly occurring wood borers, bark and shoot beetles, and root rot agents have been identified on dying trees (Dobbertin, 1999; Rigling et al., 1999; Carron, 2000). Anyway, most of this biotic agents usually behave as secondary pathogens affecting trees already under stress.

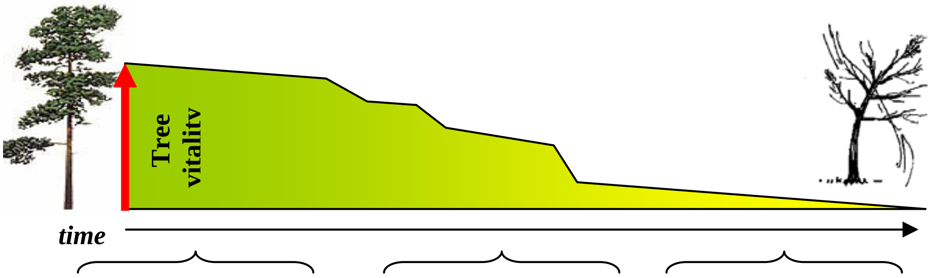
Recently, drought periods from April to June and mean temperature from April to August were found to be the most significant variables (both negatively correlated) explaining pine tree growth (Oberhuber et al., 1998; Rigling and Cherubini, 1999). Periods of high needle loss have also been found to coincide with periods of prolonged drought (Pouttu and Dobbertin, 2000). In nearly all reports on pine decline in the inner-alpine valleys, drought has been reported prior to the decline episode and considered as a triggering factor (Kienast, 1982; Vertui and Tagliaferro, 1998; Cech and Perny, 1998; Rigling and Cherubini, 1999; Dobbertin, 1999), possibly making the trees more susceptible to insect attacks and nematode or pathogen infections (Bale et al., 2002).

Most authors do not consider drought as the main factor in the decline, as Scots pine is known to be very drought-resistant and other less drought resistant trees are not affected (Vertui and Tagliaferro, 1998; Cech and Perny, 1998; Rigling and Cherubini, 1999). Even so, prolonged drought is reported to have a strong influence on young seedlings (Wittich, 1955). Unbalanced water relations may also lead to disturbed nutrient utilization and growth, resulting in abnormally reduced foliage, depressed seed production and viability, death of tree top and consequent disorders in growth and defective habitus (Schwerdtfeger, 1957). The effects vary between developmental stages of the stand, being more marked after crown closure, a critical period with diminished opportunities for trees to meet increased moisture requirements (Sokolov, 1961).

It is well-established that drought is increasing the susceptibility of pines to secondary pathogens and that warm spring and summer temperatures are increasing the reproductive rate of bark beetles (Wermelinger and Seifert, 1998, 1999) and pine wood nematodes (Rutherford and Webster, 1987; Bakke et al., 1991; Tomiczek, 1996). Prolonged drought and increased summer temperature have also been reportedly amplifying the influence of mistletoe (*Viscum album* L.), which can increase high water stress experienced by pines and whose infection rates can be as high as 80% (Dobbertin et al., 2005). Since pine growth in the Alps is strongly limited by high temperatures and summer rain shortage (Kienast et al., 1987; Rigling et al., 2003; Weber et al., submitted), climate warming may have negative effects on pine vitality, leading to a shift in the complex balance between trees and secondary pathogens.

Edaphic limitations have been also linked to growth decline, crown reduction and tree mortality, especially on serpentine-derived soils characterized by an unbalanced availability of nutrients (Oberhuber et al., 1998). Mismanagement of the forest, frequent in private lots at a low elevation, might have negatively affected tree health, especially because of a lack of thinning treatments (Vertui and Tagliaferro, 1998). The increasing competitiveness of broadleaved species in some Scots pine stands may also be the result of natural succession of the coenosis. This process may have been somewhat accelerated by the abandonment of land management practises that used to favor pines rather than more tolerant broadleaves (Rigling et al., 2006).

The global temperature rise and, even more, the alteration in precipitation regimes triggered by climate change-related processes (Price and Haslett, 1995; Hasenauer et al., 1999; IPCC, 2001, 2007; Schar et al., 2004) may contribute to pine dieback either in a direct way, i.e., influencing growth rates and causing severe physiological stress (Kienast, 1982; Kienast et al., 1987; Oberhuber et al., 1998; Dobbertin, 1999; Pouttu and Dobbertin, 2000; Rigling et al., 2002, 2003; Rebetez and Dobbertin, 2004; Weber et al., submitted), or indirectly through its influence on population dynamics of secondary pathogens and insects, or still by altering frequency and intensity of fire events (Rutherford and Webster, 1987; Bakke et al., 1991; Tomiczek, 1996; Wermelinger and Seifert, 1998, 1999; Bale et al., 2002). Conceptual interaction models have been proposed to explain the causes of tree dieback (Rigling et al., 2006) [Figure 5], but quantitative predictions of tree survival are still lacking.



Predisposing factors	Triggering factors	Proximal factors
Tree ageing		
Intraspecific competition		
Generalized drought*	Drought periods*	
Mistletoe infestation*		Mistletoe infestation*
Feeding substrate	Feeding substrate*	Feeding substrate*
(insects)*	Root rot	Bark/shoot disease*
	Vascular disease*	
		Nematodes*

*Figure 5 – Interaction of dieback factors in Sots pine forests of the Alps; factors marked by * are likely influenced by climate change (from Rigling et al., 2006).*

The modeling approach

Before developing management strategies for a sustainable development of mountainous landscapes, we need to understand the natural and human history of our ecosystems. It has been recognized that assessing, analyzing and modeling stand structures and their development are prerequisites for understanding and managing mountain forests (Schönenberger and Brang, 2001). Moreover, a better understanding of past, current and prospective stand dynamics would enable to distinguish anthropogenic negative impacts from natural variation, in the face of the recent threats posed to the stability of Scots pine stands.

On one hand, recognition of changes in ecosystem function and dynamics is possible only if sufficient data are available and relationships between different ecosystem parameters are sufficiently understood (Krauchi et al., 2000). Monitoring activities combined with experimental studies may help assessing and understanding cause-effect relationships of the major processes and feedbacks in mountain ecosystems.

On the other hand, in order to assess current stand condition and forecast its future development, an integrated model of stand dynamics is needed, that could also project the effects of past and present land use and evaluate the impact of climate change scenarios. Modeling can be seen as part of a system dynamics approach, which focuses on those factors and processes that are responsible for the dynamics of the system. Modeling means trying to capture the essence of a system, deconstructing complex interactions until only the most essential structures and processes remain (Starfield et al., 1990; Grimm et al., 1996; Haefner, 1996). The starting point is to collect the relevant information about the behavior of the system and the end point is a simulation model that enables scenarios with different assumptions to be analyzed. Simulation models describe how the state variables of a dynamic system change due to processes, which are quantified by certain parameters. Once simulation models addressing case studies of sustainable forest management have been produced and evaluated, the lessons learned from these models are likely to assist in developing indicators for other types of forests and problems as well (Brang et al., 2002).

A large number of growth models for Scots pine has recently been developed in Europe, either as single predictive equations for individual or stand growth (Stoll et al., 1994; Hökkä et al., 1997; Makela and Vanninen, 1998; Prévosto et al., 2000; del Rio et al., 2001; Andreassen and Tomter, 2003; Palahi and Grau, 2003; Jakobsson, 2005; Diéguez-Aranda et al., 2006) or as integrated suites of functions at the scale of the individual tree, stand or landscape (Deutschman et al., 1997) [Table I.1].

Model name	Resolution	Reference
EFISCEN	Size class	Sallnäs, 1989
FORSKA	Patch	Prentice and Leemans, 1990
SIMA	Patch	Kellomäki et al., 1992
FINNFOR	Tree	Kellomäki et al., 1993
FORCLIM	Patch	Bugmann, 1994
MOSES	Tree	Hasenauer et al., 1994
BIOMASS	Tree	McMurtrie et al., 1994
PROGNAUS	Tree	Monserud and Sterba, 1996
MELA	Stand	Siitonen et al., 1996
SILVA	Tree	Kahn and Pretzsch, 1997
BWIN	Stand	Nagel, 1997
FORGRA	Patch	Jorritsma et al., 1999
CAPSIS	Tree	De Coligny et al., 2002
MOTTI	Tree	Hynynen et al., 2002
FORRUS-S	Patch	Chumachenko et al., 2003
GESMO	Stand	Diéguez-Aranda, 2004
SPINE/PINUSMIX	Tree	Palahí et al., 2006
EFIMOD	Tree	Chertov et al., 2006

*Table I.1 – Model suites of forest dynamics developed in Europe and including Scots pine among the target species. Resolution refers to the spatial scale representing the model unit. Both the empirical/statistical and process-based/mechanistic approaches (*sensu *Bossel, 1991) are included.*

Nevertheless, these tools still have many limitations in predicting stand development and projecting management goals when exogenous disturbances and change dynamics are involved. Gap or successional models are able to predict the impacts of global change on long-term dynamics of forest structure, biomass, and composition (Bugmann, 2001). However, the physiology-based functions and parameters they are based upon are often difficult to estimate, and limited effort has been spent on the formulations of tree establishment and mortality, although these processes are likely to be just as sensitive to global change as tree growth itself. Individual-based empirical models, on the other hand, may be applied over a limited geographic extent, their parameters varying according to limited areas or species' ecotypes. The singular climate and site conditions characterizing southern Alps suggest the need for a localized prediction model able to integrate dynamics at the stand and tree scale with the effect of management options, and flexible enough to give reliable predictions even when long-term changes in stand structure and stability are to be forecasted.

Aims of the study

The present research is aimed at developing a modeling framework for Scots pine forests in the Alps. To this extent, the following knowledge gaps are to be addressed:

1. A lack of study areas in natural stands of Scots pine, allowing long-term monitoring of forest dynamics and providing standardized data to use for model building;
2. A limited understanding of endogenous and exogenous dynamics in Scots pine stands of the Alpine region. Using patterns and processes typical of other ecoregions to forecast paths of stand development may result in erroneous predictions or in the discounting of fundamental interactions.
3. A lack in modeling tools capable to forecast stand development on a large scale, combining endogenous and exogenous stand dynamics but at the same time allowing easy implementation of management strategies.

Answering to these needs clearly requires a multiscalar approach. Individual trees have represented the most logical modeling unit for years, but there are important processes operating at scales imperceptible to a single organism, a feature Roberts (1987) highlighted in his dynamical systems approach to ecosystems. Moreover, the relevant compositional, structural, and functional gradients emerge not only from a specific moment in time, but as a reflection of long-spanning pattern and processes (Bragg et al., 2003). Rather than developing a hierarchically structured model (Luan, 1996; Robinson and Ek, 2000; Karev, 2006), we chose to focus our analysis on a component of forest dynamics whose influence is fundamental as much for individual tree growth as for stand development and succession, and that could therefore be analyzed on different hierarchical levels at the same time: competition and mortality.

These natural processes, which operate simultaneously and interact at multiple scales, correspond to spatial (and/or temporal) patterns and structures that can be observed over a continuum of scales. When it is known that the phenomenon under study is structured as a nested series of spatial scales, this helps us understand and explain the mechanisms producing the observed patterns (Bellehumeur and Legendre, 1998).

The structure and dynamics of plant communities is governed by the endogenous process of competition between individuals (Tansley, 1920), defined as the interaction between neighboring plants induced by the necessity to share limited resources, leading to a reduction in survivorship and/or growth (Clements, 1929; Grime, 1979; Oliver and Larson, 1996). A rise in competition intensity implies a higher susceptibility to mortality factors, pulls reproductive age farther in time, hampers individual growth, controls the frequency and intensity of seed production, thus influencing population dynamics of the future generations (Pyke and Archer, 1991). Species-specific differences in life history traits, such as growth form and growth rate or the extent of shade tolerance, drought tolerance and frost resistance of saplings and adult trees play a dominant role in the competition processes of a forest stand (Waring and

Schlesinger, 1985; Otto, 1994; Schweingruber, 1996; Kimmins, 2004; Weber, 2005).

Mortality occurs when a tree's capability to contrast competitive stress through a plastic response is overcome (Hutchings and Budd, 1981; Peet and Christensen, 1987). The influence played by competition on individual survival and reproductive ability is expressed, at the higher hierarchical level, in the density-dependent regulation of plant populations, which in turn determines species presence and abundance in the community, their structure and spatial distribution or pattern. The mortality caused by competition among trees within a stand is called self-thinning (Yoda et al. 1963). Trees at a competitive disadvantage die from crowding and suppression as crowns expand and tree size increases (Long and Smith, 1984; Long, 1985). Thus, self-thinning refers to the reduction in tree numbers over time due to density-dependent mortality as the plants increase in size (Yoda et al. 1963; Sackville Hamilton et al., 1995; Kikuzawa, 1999; Hedin, 2006). One result is the existence of an upper limit to the average size of a given number of trees or plants that occupy an area (Reineke, 1933; see also the review in Reynolds and Ford, 2005).

Competition dynamics are not directly measured. Systematic studies to isolate and understand the principles underlying competition at the individual level began in the 1950s; recent research on natural and experimental communities has shown that the most effective way of understanding competition is to study it from the point of view of a focal or target plant and the characteristics of its perceived neighborhood (Pacala and Silander, 1985; Kenkel, 1990; Stoll and Weiner, 2000). On a stand scale, self-thinning dynamics have been seldom examined in European forestry (Daniel and Sterba, 1980; Sterba, 1981, 1985, 1987; Hynynen, 1993; Del Rio et al., 2001; Palahi et al., 2002; Monserud et al., 2004; Anta and Gonzalez, 2005; Pretschz and Biber, 2005; Vacchiano et al., 2005). Nonetheless, some authors stressed that analysis of self-thinning helps assessing competition in forest stands and building individual or stand-based models mimicking plant community dynamics (Sterba and Monserud, 1997).

Therefore, simultaneous analysis of competition effects on both the individual and the stand scale can be considered as important steps towards a greater understanding of specific stand and population dynamics. The outputs of these multiscale studies can be profitably nested in a hierarchical way, either to provide a source of validation for emergent properties such as density-dependent mortality (Robinson and Ek, 2000; Monserud et al., 2004), or to supply multiple input for composite models of forest development. The following three chapters address research questions related to modeling of stand dynamics in Scots pine forests in the Alps, with a particular focus on competition and mortality.

Chapter II details the development of tools intended for modeling stand development at a regional scale and guide silvicultural management decisions. Such framework will be based upon relevant ecological and biometric relationships and will allow the forecasting of future stand development based on current stand structure. The model will be able to aid in the description of silvicultural goals and in the identification of the management strategy most suitable to achieve them, even in the context of exogenous change scenarios.

Chapter III will focus on competitive dynamics at the plot- and individual tree scale. The establishment of a network of permanent plots in Scots pine stands will be detailed, along with the results from the first field measurements. We will analyze the influence of intra- and interspecific competition on tree growth and survival, and the response of such dynamics to land use history. The study will show the results of the integration of independent methods of analysis, i.e., use of historical archives, dendrochronology, spatial statistics and growth modeling. Information coming from the described sources will concur to give a dynamic picture of past and future development of stands differing for site conditions, history, structure and composition.

Chapter IV is the result of cooperation with researchers from Utah State University and the USDA Forest Service. A joint project is currently underway, aiming at validating a stand growth and yield model with a nationwide inventory of target forest communities. Participation in this process has brought the chance of de-constructing the structure of a complex modeling software, whose usability and flexibility to user's input are among the desired features of a species-wide prediction model for Scots pine dynamics. This chapter will detail model functioning and provide examples of model calibration against existing stand inventory data.

Consideration about possible uses and data needs of such a model in a European context will follow in the conclusive chapter. Results from integrating analysis of competitive dynamics over different scales will be presented there. Finally, directions for further research aiming at implementing a full stand dynamics model for Scots pine will be suggested.

Chapter II: A Density Management Diagram for Scots pine in the Western Alps[1]

Introduction

Scots pine forests in the western Alps have recently undergone great changes in both extent and stand structure (Vacchiano et al., 2006a). Dynamics such as secondary succession following land abandonment on one hand, and the yet unexplained dieback wave in Scots pine stands on the other, force managers to modify traditional silvicultural planning for the species, in order to continue the pursuit of desired forest functions and guarantee the sustainability of their delivery.

In order to harmonize management needs over vast areas, the dynamics regulating stand stability and vegetation development over time must first be investigated at the species level. Density Management Diagrams (DMD) are graphical models of even-aged stand dynamics (Newton, 1997). They reflect fundamental relationships involving size, density, competition, site occupancy, and self-thinning (Jack and Long, 1996). They allow users to forecast stand development based on allometric relationships, and they portray basic competition and mortality dynamics for single species stands. They are also extremely useful in displaying and evaluating alternative density management regimes intended to accomplish diverse objectives (Shaw and Long, in press).

Jack and Long (1996) and Newton (1997) gave useful reviews of the history and features of DMDs; such diagrams exist for a number of species in North America (Drew and Flewelling, 1979; McCarter and Long, 1986; Hibbs, 1987; Long et al., 1988; Kershaw and Fischer, 1991; Dean and Jokela, 1992; Dean and Baldwin, 1993; Williams, 1994; Archibald and Bowling, 1995; Farnden,

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[1] To be submitted as Vacchiano G., Long J.N., Motta R. (2006), *A Density Management Diagram for Scots pine in the Western Alps*.

1996; Sturtevant et al., 1996; Smith and Woods, 1997; Newton, 1998; Saunders and Puettmann, 2000; Spathelf and Schneider, 2000; Long and Shaw, 2005; Mack and Burk, 2005; Newton, 2006; Sharma and Zhang, in press; Shaw and Long, in press), Central and South America (Márquez-Linares and Alvarez-Zagoya, 1995; Chauchard et al., 2001, 2003), Asia (Ando, 1962, 1968; Tadaki, 1963; Kumar et al., 1995; Yoshimoto, 2003), and Africa (Onyekwelu et al., 2003; Biber et al., 2004), but with a couple of exceptions (Sales Luis and Fonseca, 2004; Anta and Gonzalez, 2005) they have never been developed for any European species. The aim of this research is to develop a DMD for Scots pine in a defined geographic context, i.e. the western Italian Alps, and test its suitability for:

1. Rapid assessment of stand structural conditions;
2. Forecasting of future stand development;
3. Comparing the effectiveness of different silvicultural management strategies;
4. Modeling the impact of exogenous dynamics and the response of forest stand to scenarios of future change.

We designed several management scenarios to test the effectiveness of the diagram in modeling the delivery of important forest functions. Management aims were characterized by quantitative structural parameters and plotted on the DMD, in order to evaluate the silvicultural measures needed to reach them.

Assumptions

Density Management Diagrams are practical tools, describing average stand dynamics and allometric relationships over a wide range of stand ages and structures. They are not intended do portray detailed or individual growth functions; some assumptions must therefore be drawn to ensure their applicability (Jack and Long, 1996; Long et al., 2004; Reynolds and Ford, 2005):

I. Monospecific, even-aged stands or cohorts develop from a collection of individual, free to grow trees through the onset of competition, to full site occupancy, self-thinning, and the eventual development of multicohort stand structures (Oliver and Larson, 1996; Long et al., 2004) [Figure 6].

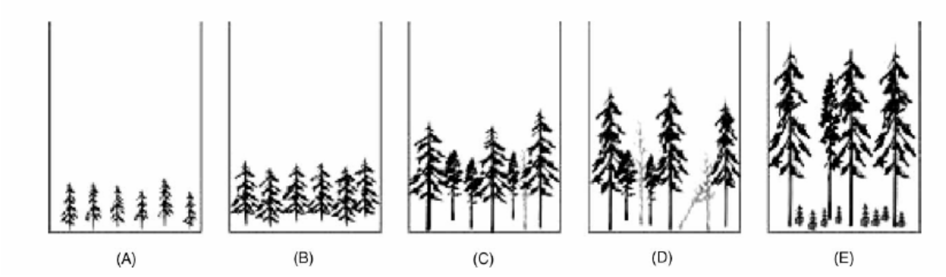

Figure 6 – Stages of stand development for an idealized even-aged stand. (A) Trees are free-to-grow; (B) onset of competitive interaction; (C) full site occupancy; (D) self-thinning; (E) stem reinitiation (Long and Smith, 1984).

II. Self-thinning is predictable and conservative, i.e., the lines representing the maximum size-density boundary and the onsite of self-thinning are assumed to be correct for all sites (Jack and Long, 1996) and constant at least within the species' level (Shaw, 2006).

III. Allometric relations are assumed to hold for unthinned stands independently of site quality (Assmann, 1970); changes following artificial thinning are short-lived and do not change allometric functions during stand development (Drew and Flewelling, 1979; but see Cameron, 1988; Farnden 1996).

IV. Relative density, derived from tree size and number, effectively indexes competition and site occupancy dynamics (Curtis, 1970) and is independent from age and site fertility (Reineke, 1933).

V. No mortality is assumed to take place prior to the onset of self-thinning; deaths resulting from density-independent factors (e.g., disturbance or biotic agents) are not predictable by this kind of model and therefore disregarded. In other words, stands are assumed to grow relatively undisturbed until density-related mortality begins (B.C. Ministry of Forests, 1997).

VI. The diagrams are built upon long-term average dynamics. Limited short-term data series, such as yearly growth data or once-repeated mortality assessments, may not fit on the model due to local spatio-temporal variability (e.g., climate influence on growth, pest outbreaks, etc.).

VII. Spatial distribution of individual trees is not taken into consideration. Some authors used different DMDs for planted and natural stands, trying to account for the local heterogeneity of mortality rates due to tree clumping (Farnden, 1996). This effort is not undertaken herein.

VIII. The diagram simulates only dynamics related to the structural development of the forest stand; processes regarding understory development, fuel loads, habitat requirements such as coarse woody debris availability, water regimes, etc. are not directly estimated.

IX. Non-timber forest functions can be associated to relative density or average size/density targets. Nonetheless, the outcome of the comparison between average stand conditions and management objectives has a strictly binary character (yes/no), and does not allow for smooth transitions.

X. Applicability of the DMD is strictly limited to stand structures similar to the ones it was built with. It would be possible to apply the diagram to discrete even-aged cohorts in a multi-aged stand, but extending the DMD and its allometry to mixed or irregular structured stands as a whole, or beyond the geographic range it implies, is not recommended.

Methods

Stand inventory

A regional forest inventory (IPLA 2003a, 2004) provided the data necessary for the construction of the DMD. The inventory is based upon a network of temporary plots set up with a variable-distance grid. Base grid size is 500 m; effective sampling distance ranges from 316 to 1414 m, each plot representing a surface of 10 to 200 ha according to forest cover type and timber potential of each stand. Sample plots are circular in shape, with a radius between 8 and 15 m according to overstory density. In each plot, the following site and stand-level variables were recorded: geographic coordinates, elevation, average slope, forest cover type, stand structure and developmental stage, percent canopy cover, number of stumps and snags, seedling count, forest health conditions, recommended management goals and priorities. Species and dbh (to the nearest cm) of all living individuals bigger than 7.5 cm in dbh were recorded. In each plot, total height to the nearest m was measured for the tree with maximum dbh.

The database encompassed 457 plots where Scots pine forest cover type was recorded. Stand density, basal area on a per hectare basis and quadratic mean diameter (QMD) were computed for Scots pine and for all species combined. We calculated Reineke's (1933) Stand Density Index (SDI) according to the following formulations, as modified by Daniel et al. (1979b) [1] and Long and Daniel (1990) [2]:

[1] $$SDI_{Dq} = N \cdot \left(\frac{QMD}{25} \right)^{1.6}$$

[2] $$SDI_{sum} = \sum \left(N_i \cdot \left(\frac{D_i}{25} \right)^{1.6} \right)$$

where SDI is Stand Density Index,

QMD is quadratic mean diameter at breast height [cm],

N is the number of trees per hectare,

D_i is breast height diameter of the *i*-th tree on the plot [cm],

N_i is the number of trees per hectare represented by the *i*-th tree.

The two methods have been shown to produce values of SDI that are essentially equal for even-aged stands, but increasingly divergent with increasing skewness of the diameter distribution (Shaw 2000). Ducey and Larson (2003) quantified the relationship between SDI_{sum} and SDI_{Dq} using a Weibull model and showed that the ratio of the two values approaches 1 for stands that are even-aged (i.e., diameter distribution weighted heavily about the mean diameter). Therefore, we calculated the ratio of SDI_{sum}:SDI_{Dq} for the purpose of separating relatively even-aged stands from stands with more complex structures.

Plot selection

For the construction of the DMD and the evaluation of its inherent allometric relationships, inventory plots were selected according to the following criteria (Shaw and Long, in press):

a. Species composition (more than 70% of basal area represented by Scots pine),

b. Age structure (ratio of SDI_{sum}:SDI_{Dq} ≥ 0.9; stands recorded as having irregular structure were excluded from further analyses),

c. Management impact (number of stumps less than 20% of living stems, in order to exclude from the analysis recently disturbed stands whose growth dynamics had not yet the time to recover),

d. Sample size (more than 10 measured trees per plot).

Maximum density boundary

Among the several formats proposed for DMDs (Jack and Long, 1996) we chose to represent stand development using stand density and QMD, as a measure of mean tree size, on the major axes. Competition-driven stand dynamics for pure, even-aged stands are best described by the self-thinning law (Yoda et al., 1963), depicting the inverse-proportional relationship between plant mean size (or biomass) and stand density. In undisturbed stands undergoing severe intraspecific competition, the death of the suppressed trees is compensated by the growth of the survivors. Maximum stand density achievable for each mean individual size is plotted by an exponential function. Comparing observed stand density against the theoretical maximum expressed by this self-thinning line, one can easily assess the intensity of competition acting in the stand and predict its outcome in terms of tree mortality and stand structural features (Long and Smith, 1984).

We chose to represent the self-thinning boundary as a log-linear relationship between QMD and density (Reineke, 1933), since these were the parameters more readily available in the referenced forest inventory. Several authors reported for older stands the evidence of a fall-off from the size-density boundary (White and Harper, 1970; Jack and Long, 1996; Cao et al., 2000;

Zeide, 2005). They attributed this pattern both to the inability of old, large trees to fully recapture available resources following the death of other large trees, and to crown shyness proportionally increasing with tree heights (Putz et al., 1984; Long and Smith, 1992). No evidence of this "Mature Stand Boundary" (Shaw and Long, in press) has been provided so far for Scots pine. Data used in this study could not either prove or disprove the hypothesis, which was therefore disregarded in subsequent analyses.

Accurate determination of the self-thinning trajectory for any population remains a difficult task, especially using temporary plots as a data source. First, in a given sample only a fraction of stands are actually in a true self-thinning mode. The rest are understocked for a number of reasons, e.g., insufficient regeneration density or intense disturbance impact (Tang et al., 1994; Wirth et al., 1999; Shaw, 2006). Second, many investigators have determined that the self-thinning slope should be a species-specific parameter (Weller, 1987; Hynynen, 1993, Pretzsch and Biber, 2005), while others have found no evidence that the slope should differ from Reineke's suggested 1.6 (Long and Shaw, 2005).

In this study, Reineke's SDI [1] was calculated for each plot first assuming a constant self-thinning slope of 1.6, represented by the power coefficient in equations 1 and 2. Maximum SDI was assumed to be the 98th percentile of the SDI frequency distribution; higher SDI can be attained by extremely dense sample plots (or due to sampling errors), but the stand's and species' SDI generally has a less extreme value. Analysis of known SDI_{max} values and inventory data for several forest species in the Western US showed that the 98th percentile of the SDI frequency distribution is a reliable threshold for SDI_{max} estimation at the stand or population level (Shaw, pers. comm.). An exponential function with power equal to 1.6 was fitted through density and QMD values representing an SDI equal to SDI_{max}. Relative density (RD), expressed by the ratio between plot-level SDI and SDI_{max}, gave an estimate of overall competition intensity in the stands.

In order to test for a variable slope, a new regression line was subsequently fitted between the most crowded stands. To ensure that only stands actually undergoing self-thinning were selected, a minimum threshold of RD = 0.70 was maintained (Solomon and Zhang, 2002), both including and excluding the “tail” of the SDI distribution. The negative slope of the new self-thinning line was then compared with Reineke’s slope (1.6) at a 95% confidence level.

Relative density lines

Estimates of stand density are made to express the degree to which the free growing space[2] is utilized for tree growth. The self-thinning line represents maximum achievable density for every given mean size, i.e., maximum exploitation of available growing space, and therefore maximum competition intensity. The use of SDI as a relative density index is strongly encouraged by its independence from stand age and site fertility (Reineke, 1933; Long, 1985). Lines representing fixed fractions of SDI_{max} were plotted in order to readily assess RD of current and projected stands. Stands with the same relative density share many fundamental population-level attribute, including self-thinning, canopy closure, mean live crown ratio, and growth-growing stock relationships (Jack and Long 1996). Different RD thresholds have been suggested to indicate crown closure, initiation of competitive dynamics, and the onset of self-thinning (Drew and Flewelling, 1979; Long, 1985). These key values [table II.1] will be used to infer current and future stand dynamics and guide silvicultural prescriptions.

We used ancillary data to test the validity of some of the described dynamics in Scots pine stands. In particular, mean live crown ratio (LCR) measured in 8 permanent plots (Vacchiano, 2007c), as well as canopy closure estimates to the

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[2] Growing space refers to the availability of all resources needed by a tree to exist on a given site. A deficiency of any of these resources may limit the growing space (Smith, 1986), and hence affect tree growth. For individual trees, growing space is often defined in terms of the horizontal dimensions of available ground surface area or crown projection area (Spurr, 1952; Assmann, 1970; O'Hara, 1988).

nearest 10% from the temporary plot network, were linearly related to Relative Density of the respective stands.

RD	**Stand structure and dynamics**
0-25%	Open-grown trees. Individuals are free from neighbor influence and attain maximum crown width and individual increment.
25-35%	Canopy closure phase. Crowns begin touching each other, setting the onset of intraspecific competition. Self-pruning and size class differentiation accelerate, and the plastic response of tree growth to density is expressed.
35-60%	Full site occupancy is reached. Trees in the stand can no more access site resources at full potential, and individual increment suffers significant reductions. Net stand growth is maximized.
60-100%	Zone of imminent competition-related mortality (ZICM). Plastic adaptations in growth can no longer compensate the decreased resource income. Starting from the lower size classes, trees die as a result of competition. Gross stand increment and total yield are maximized, but a variable amount of growth is intercepted by mortality, reducing net total growth.

Table II.1 – Relative density thresholds representing stand developmental stages (from Long, 1985).

Allometric relationships

Dominant height is, from a biological point of view, the best index for establishing the thinning intervals for this species (Duplat, 1996). If correctly coupled with site index curves (see after), dominant height can be used to assess the time projected stands require to reach a certain position on the diagram. Since we could not rely upon multiple stand height measurements, we use the height of the thickest tree in the plot as a surrogate for dominant height.

For a particular height, trees that grow in high density stands will have smaller diameters than those growing in less dense stands, because of greater competition among individuals (Zeide, 1993; Staudhammer and LeMay, 2000). Even if the H-D relationship for dominant trees should be less influenced by density (Assmann, 1970), we included all the three variables in the following nonlinear model [3], which represents a modification of the one proposed by Shaw and Long (in press) for longleaf pine in the US:

$$QMD = 7.5 + (a + bN)(H - 1.3)^{c} \qquad [3]$$

where QMD is quadratic mean diameter at breast height [cm],

N is number of trees per hectare,

H is the height of the dominant tree on the plot [m],

a, b and c are model parameters.

Model form was chosen to reflect the density-related effect on the H-D relationship (constraining a negative *b* coefficient); the 7.5 cm intercept was forced to account for the minimum dbh measurement threshold. Number of parameters was kept as low as possible, accorded that regression parameters were significant at the 95% confidence level.

Mensurationists responsible for the regional forest inventory also gave indications about single-tree volume, using parabolic functions of dbh that were parametrized according to site fertility class. We used such volume predictions to calculate stand volume on a per-hectare basis for each plot. Total stand yield was then expresses as a function of the other DMD variables [4], in order to evaluate stand volume exploited by the proposed management strategies:

$$VOL = aN(QMD)^{b} \qquad [4]$$

where VOL is total standing volume [m^3 ha^{-1}],

QMD is quadratic mean diameter at breast height [cm],

N is number of trees per hectare,

a and b are model parameters.

The model is a 2-parameter modification of Long and Shaw's (2005), and has been previously used by yield tables for Scots pine in some Italian regions (Tabacchi et al., 2000). Both models were fitted using the nonlinear regression module of SPSS (SPSS Inc., 2003); we assessed goodness-of-fit by calculating adjusted R^2 and standard error. We tested independence of model residuals from prediction variables and other stand and site parameters. Data from 8 permanent plots (Vacchiano, 2007c) were plotted on the DMD and used to validate the fitted functions.

Results

Stand variables were analyzed and plotted in various combinations in an effort to identify unusual conditions and outlying values. Average stand variables were not normally distributed among the plots: we noticed a lack of very young, dense stands (density > 1500 trees per hectare, QMD < 12.5 cm), attributable to sampling methods; this could impair statistical accuracy and applicability of the DMD for these range of stand structures.

After selection and screening, 244 sample plots [table II.2] were retained for determination of the maximum density line. Geographical distribution of the plots covered most the relevant sectors of Scots pine distribution in the study area [Figure 7]. Some parts of the species' range are underrepresented due to the high occurrence of mixed stands (Scots pine is frequently mixed with Downy oak [*Quercus pubescens* Willd.] and Manna ash [*Fraxinus ornus* L.] in the Langhe region, and with European chestnut [*Castanea sativa* Mill.] and Sessile oak [*Quercus petraea* (Mattus.) Liebl] in the Northern lake district), or because of high utilization rates (i.e., in the northernmost Ossola valleys).

	Mean	**Minimum**	**Maximum**	**St.Dev.**
Plot area [m^2]	112	50	225	39.6
QMD [cm]	21.4	10.7	50.4	5.8
Trees ha^{-1}	932	152	3318	525
Basal area [$m^2\ ha^{-1}$]	30.52	3.77	84.22	14.70
% Scots pine on BA	92.5%	70%	100%	8.3%
Height of dom. tree [m]	13.5	5	31	3.9
Standing volume [$m^3\ ha^{-1}$]*	202.47	13.18	743.43	140.89

*Table II.2 – Summary of sample plots used for the construction of the DMD. *Volume equations were available only for 118 plots.*

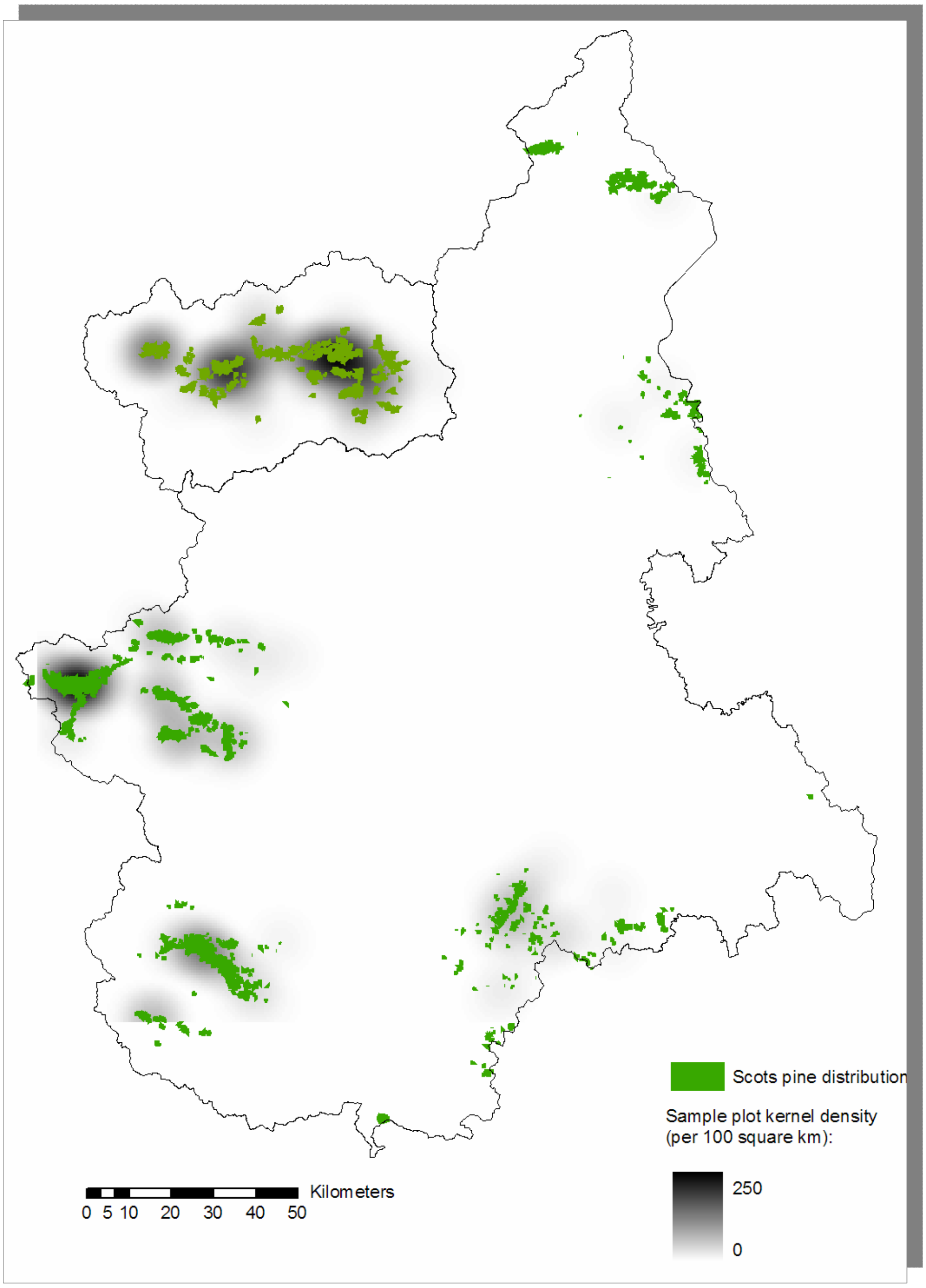

Figure 7 – Scots pine distribution in the study area and kernel density of the plots used for the construction of the DMD (number of plots per 100 km^2).

Maximum calculated SDI for Scots pine stands in the sample is 1375 [Figure 8]. Four plots had higher SDI, representing 99th and 100th percentiles of the SDI frequency distribution, and were discarded from the stand-level estimate. The range of relative densities in the sample is between 0.06 and 1.00. In most stands (48%) RD ranges between 0.35 and 0.60; 25% of the stands have a RD greater than 0.60 [Figure 9].

The slope of the self-thinning lines that were fitted by ordinary least squares regression between QMD and density of the stands with RD >0.70 were -1.65 and -1.51, respectively including or excluding from the sub-sample the plots with $SDI>SDI_{max}$ (R^2 = 0.95 and 0.94 respectively). In both cases, the confidence envelope for the new slope included Reineke's value of -1.6 ($p < 0.05$). Reineke's slope was then used in all subsequent analyses.

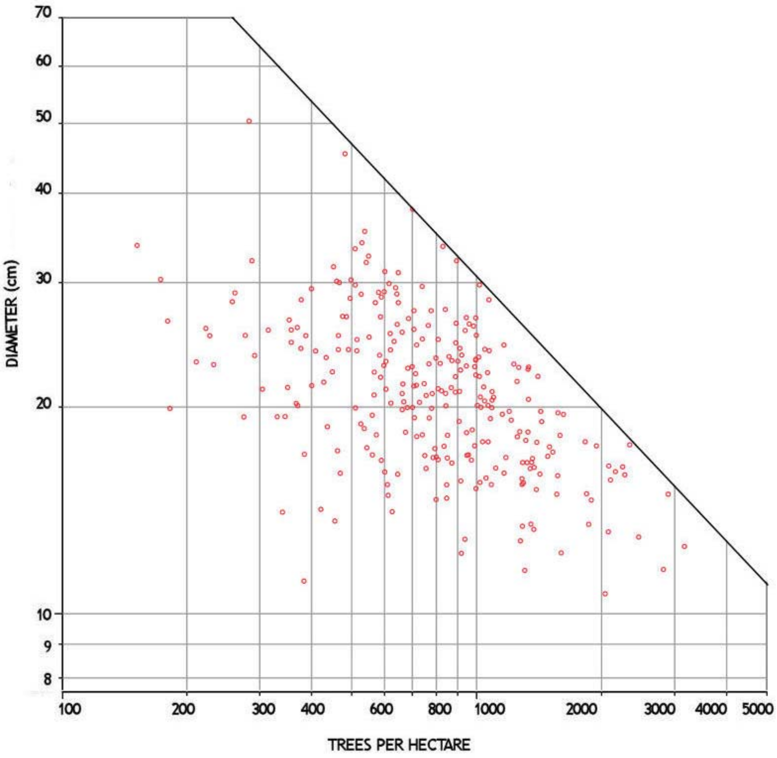

Figure 8 – QMD and density for the 244 plots included in the data set. The sloping line represents a maximum SDI of 1375.

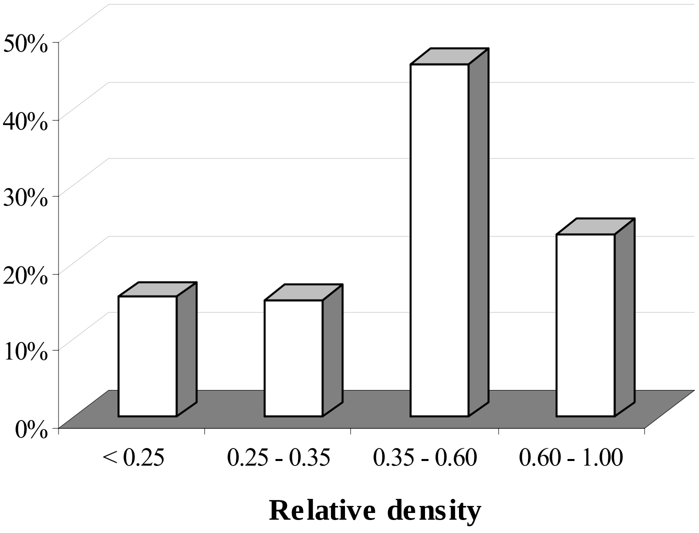

Figure 9 – Relative density frequency distribution for SDI$_{max}$ =1375. RD classes according to Long (1985); the sample is dominated by well-stocked stands.

Data from Second National Swiss Forest Inventory (WSL, 2005) report, for pure Scots pine plots (more than 70% of total basal area) in the Alpine region, a SDImax of 1348, as represented by the 98th percentile of the SDI distribution. The absolute maximum is 1620. Del Río et al. (2001) obtained a SDI$_{max}$ of 1444, although they applied a different self-thinning slope. Other referenced maximum SDI for Scots pine in Europe range from 1229 (Sterba, 1981) to 1368 (Palahí et al., 2003). Even though the datasets used in their studies show differences of origin (planted or naturally regenerated stands), treatment (untreated or lightly thinned), stocking (different initial spacing), and plot selection criteria (which are explicit only in one study), the SDI$_{max}$ seems fairly constant. We also compared the sample maximum against SDI obtained by available yield tables for Scots pine in Europe (Wiedemann, 1949; Décourt, 1965; Hamilton and Christie, 1971; Marschall, 1976; Thren, 1987; Jansen et al., 1996), computed from quadratic mean dbh and density of principal yield and removals predicted for the highest site index in each table. The estimate from the current study was 12 to 36% higher than SDI from yield tables; this can be explained assuming that the removals planned by the yield tables had a stronger effect than natural mortality in shaping future density and crowding of the stand.

We could not find any significant difference in the self-thinning slope from Reineke's suggested value of -1.6. The constancy of the self-thinning process in Scots pine was noted by Włoczewski (1968), who pointed out that the "percent elimination of trees" in given time intervals was comparable among different habitats, even if the absolute densities were not similar. According to Reineke (1933), maximum density lines of different species differ only for the intercept value; within a species, different ecotypes or site fertility levels determine a higher or lower speed of advancement along the same self-thinning trajectory. Several sources, however, suggested that maximum potential density is to be understood as a site property (Assmann, 1970; Sterba, 1987). Different site qualities, therefore, have often been characterized by different SDI_{max}, by varying either the intercept or the slope of the self-thinning line (Sterba, 1981; Hynynen, 1993; Morris, 2002; Monserud et al., 2004). A one-way ANOVA showed significant differences in mean SDI values when they were grouped by forest type (IPLA, 2003a); the Mid-continental type Scots pine plots had the higher SDI on average, followed by the Inner-alpine, the Interior Hills and the Heath forest types ($p < 0.05$). We could not draw definitive conclusions, since sample size was very small (3 to 63 data per forest type) and a comparison between the maximum SDI values rather than the mean is advisable. Therefore, we defined a single SDI_{max} value for all the plots, holding both the slope and the intercept of the self-thinning line constant.

Relative density in most Scots pine stands (75%) is less than 0.6, the lower threshold of the self-thinning zone or "zone of imminent competition mortality" (Drew and Flewelling, 1979). Land use changes played a major role; many stands established on recently abandoned areas, and even on the best sites, have not undergone self-thinning yet, but may soon be expected to do so. A relative density corresponding to 25% of SDI_{max} has generally been associated with the transition from open-grown to competing populations (Long, 1985). We suggest that an SDI of 350 be used to represent the onset of competition; this level has already been reached in the majority of stands.

Crown cover in 10% classes was plotted against SDI to test for the validity of the relationship outlined by Long (1985) [Figure 10]; 100% cover is attained at relative densities as low as 0.37, but average RD for complete closure is 0.63.

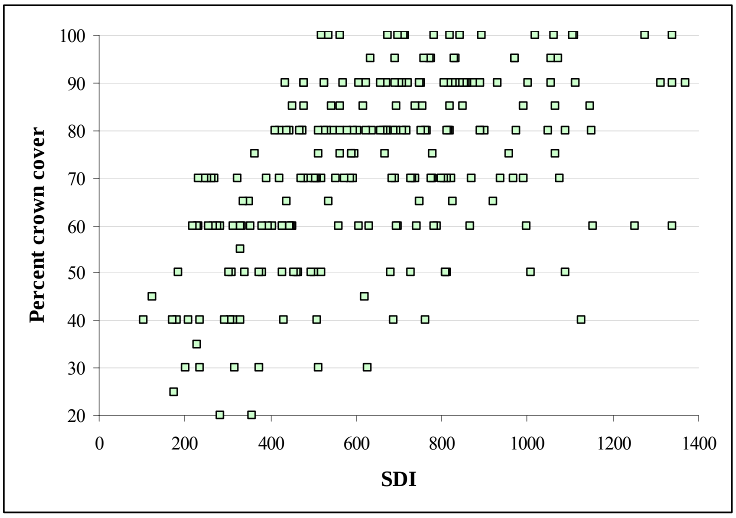

Figure 10 – Percent canopy cover as a function of plot SDI.

We assessed the relationship between stand Mean Crown Ratio (MCR) and SDI in 8 permanent sample plots established in the analyzed Scots pine range (Vacchiano, 2007c); the linear model [Figure 11] has an R^2 value of 0.54. The different incidence of pathogens on crown health (unpublished data) accounted for the poor model fit. Nevertheless, according to the average model a mean crown ratio of 0.40, recommended to maintain the tree's timely response to thinning (Daniel et al., 1979a), is attained at RD = 0.75, but in some case is reached as RD as low as 0.53. A relative density of 0.39 is associated with a MCR of 0.6, i.e., two-thirds of the bole covered by live crown.

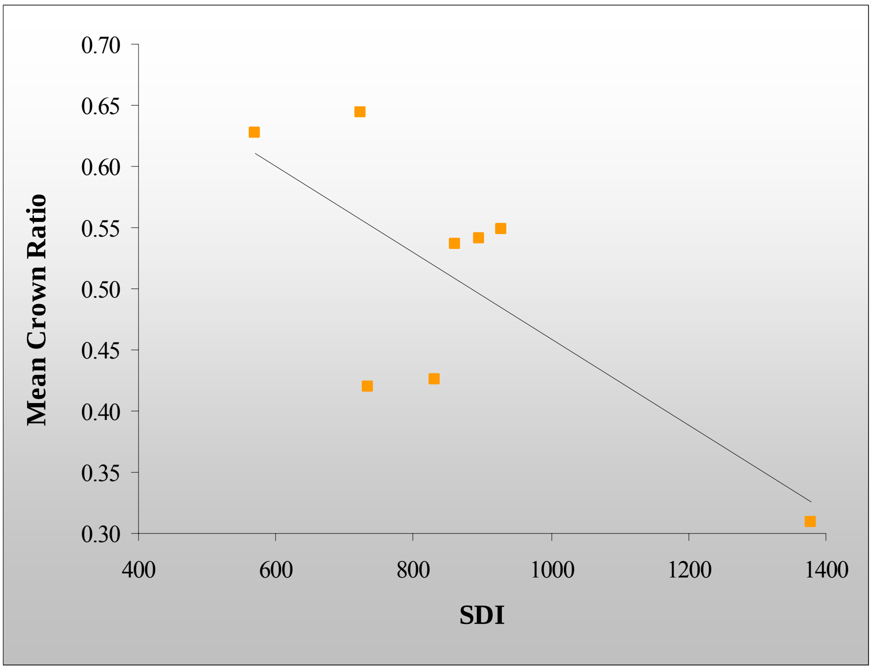

Figure 11 – Mean live crown ratio as a function of SDI in 8 permanent sample plots (see Vacchiano, 2007c for plot description).

Table II.3 summarizes best-fit estimates for equations [3] and [4], representing the allometric relationships to be included in the DMD. Residual analysis did not evidence any relevant bias against predictor variables; on the contrary, geographical plot location did prove strongly influential on model accuracy [Figure 12]. This could bring up the need of constructing separate diagrams for different locations, to better capture local variability in allometric relationships.

The calibrated models were used to generate top height and volume isolines on the DMD; the lines cover the full range of H and VOL characterizing the analyzed plots. Data from permanent sample plots (Vacchiano, 2007c) were used to validate the models, both statistically [table II.4] and graphically on the final DMD [Figure 13]. Root mean square error for dominant height was ±6.26 m, but it decreased to ±1.16 m when the two most biased study areas were removed from analysis.

Equation 3 $QMD = 7.5 + (a + bN)(H - 1.3)^c$

	a	b	c	Adjusted R^2	RMSE
Estimate	4.959	-0.0014	0.537	0.422	±4.32 m
Asymptotic SE	0.739	0.00025	0.0568		

Equation 4 $VOL = aN(QMD)^b$

	a	b	Adjusted R^2	RMSE
Estimate	$1.26*10^{-4}$	2.430	0.917	±40.11 m^3 ha^{-1}
Asymptotic SE	$2.22*10^{-5}$	0.0537		

Table II.3 – Non-linear regression fit for allometric equations [3] and [4].

Study area	N [Trees ha^{-1}]	QMD [cm]	SDI	H [m]	H_{exp} [m]	Mean bias	RMSE
Trasquera	581	29.7	766	24.2	23.9	-1.5 m	±6.76 m
Santa Maria	924	23.7	849	17.9	17.0		
Toceno	794	35.0	1360	22.7	39.9		
Borgo Ticino	370	30.6	511	24.6	22.7		
Morgex	595	25.8	626	16.7	17.2		
St.Denis I	1183	12.6	395	7.8	3.5		
St.Denis II	1814	17.2	997	14.2	14.2		
Challand	782	25.7	817	17.6	19.1		

Table II.4 – Measured and expected stand parameters for 8 permanent sample plots. Density, QMD and Dominant height were computed for Scots pine only. H_{exp}: Stand dominant height (height of the 100 thickest trees per hectare) as predicted by H isolines in the DMD.

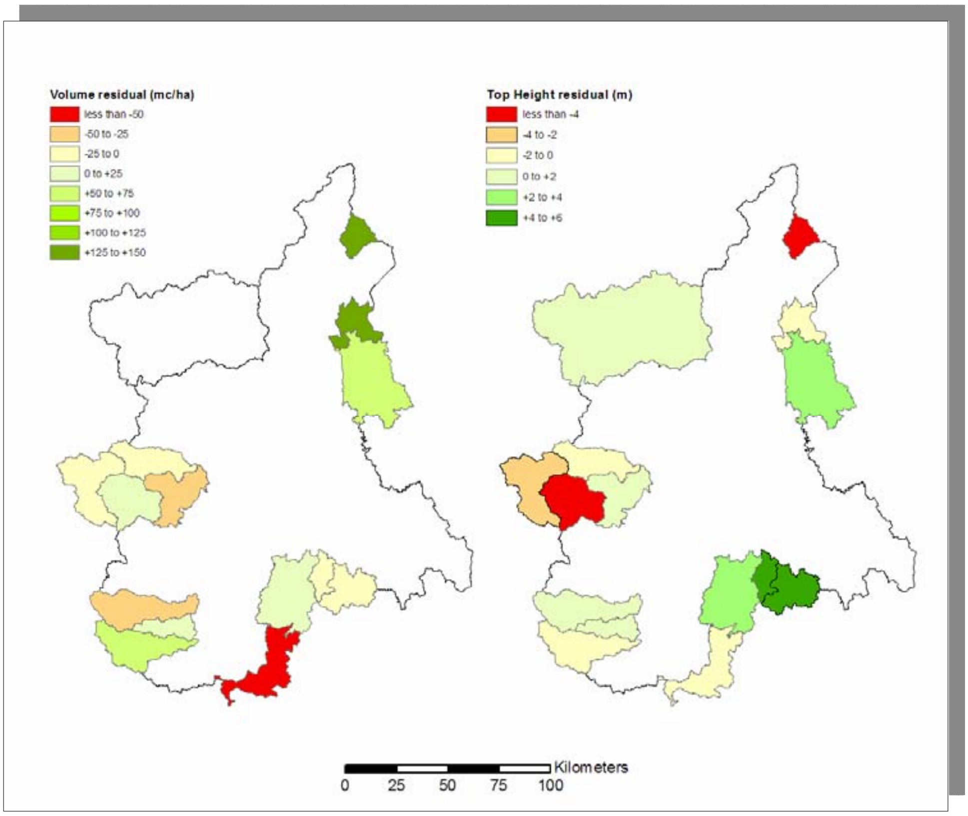

Figure 12 – Mean overprediction (red) or underprediction (green) error of allometric models for plot total volume (left) and dominant height (right), computed by forest district.

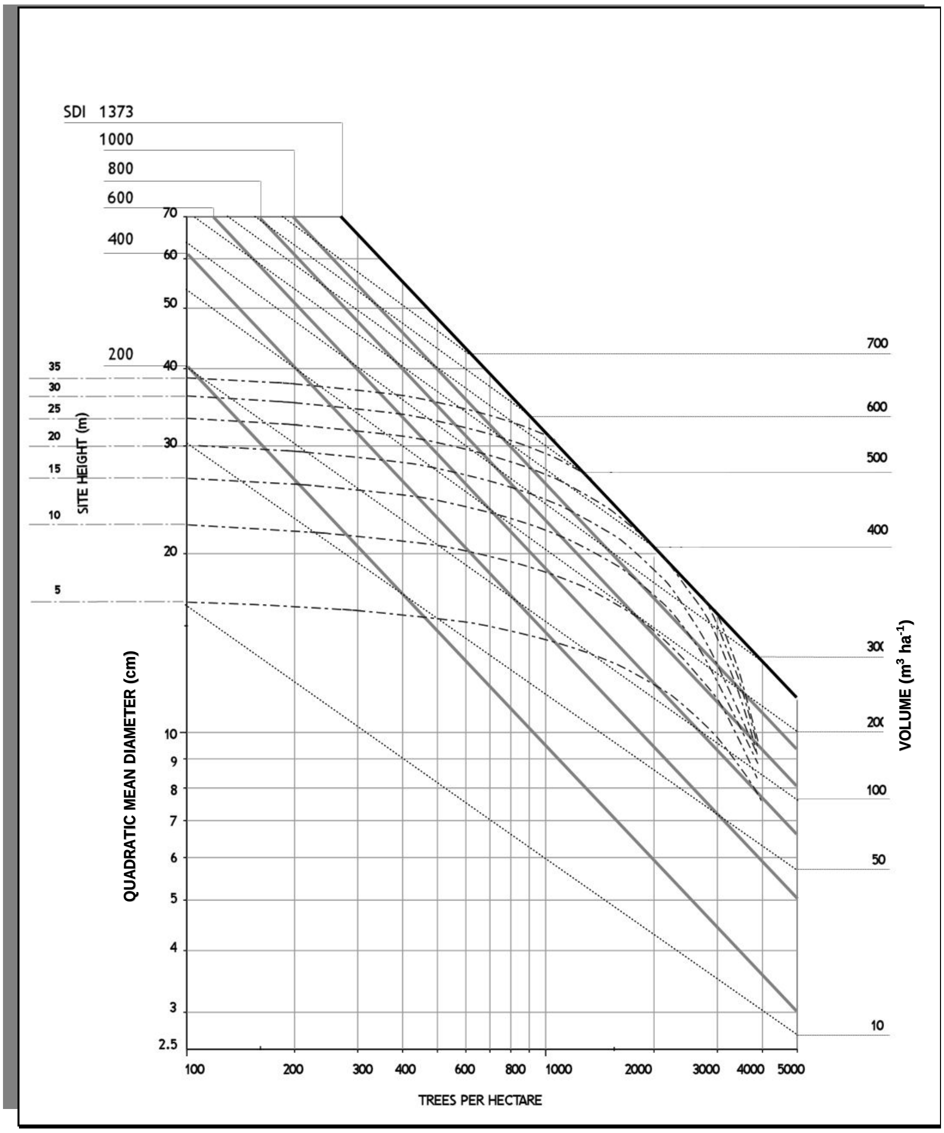

Figure 13 – Density Management Diagram for Scots pine in the Western Italian Alps.

DMD usage and testing

Density Management diagrams have two major uses: a) Plotting existing stands to assess their current structure and developmental stage, or b) developing silvicultural strategies to reach management aims defined in terms of target average tree size and density of the stand. We present a number of case studies, using either existing or hypothetic stand structures as a starting point and planning for the achievement of timber and non-timber management goals.

Case 1: Timber rotation

Only 8% of Scots pine forests in Piedmont is currently recommended for active timber management (Camerano et al., 2004). These include mostly stands growing in outer alpine sectors, on acid and sandy soils, with high precipitation (1200 to 1800 mm year $^{-1}$) and relative humidity. On these sites, standing volume at the end of rotation can be higher than 250 m^3 ha^{-1}; tree height easily reaches 20 to 25 m (IPLA, 1996) and quadratic mean diameter can be as high as 35 cm. Most of these stands are the result of secondary succession following the abandonment of pastures and meadows (Garbarino et al., 2006); all the developmental phases are represented, from dense pole stage to mature high forest.

A recently established pure stand was chosen as a case study to evaluate different silvicultural alternatives by means of the DMD. The stand [Figure 14] is located in the municipality of Santa Maria Maggiore (UTM: 457 763 E, 5 110 657 N) on an elevation of 1095 m. Details about plot establishment and field measurements can be found in Vacchiano (2006c).

The lower part of the pine forest is occupied by young, even-aged stands (average age is 40 years, as measured by core sampling). Density is around 950 trees per hectare (dbh >7.5 cm) with a quadratic mean diameter of 24 cm (Saponeri, 2006). The early developmental stage and the high density characterizing the stand allow for a timely design of an effective thinning strategy.

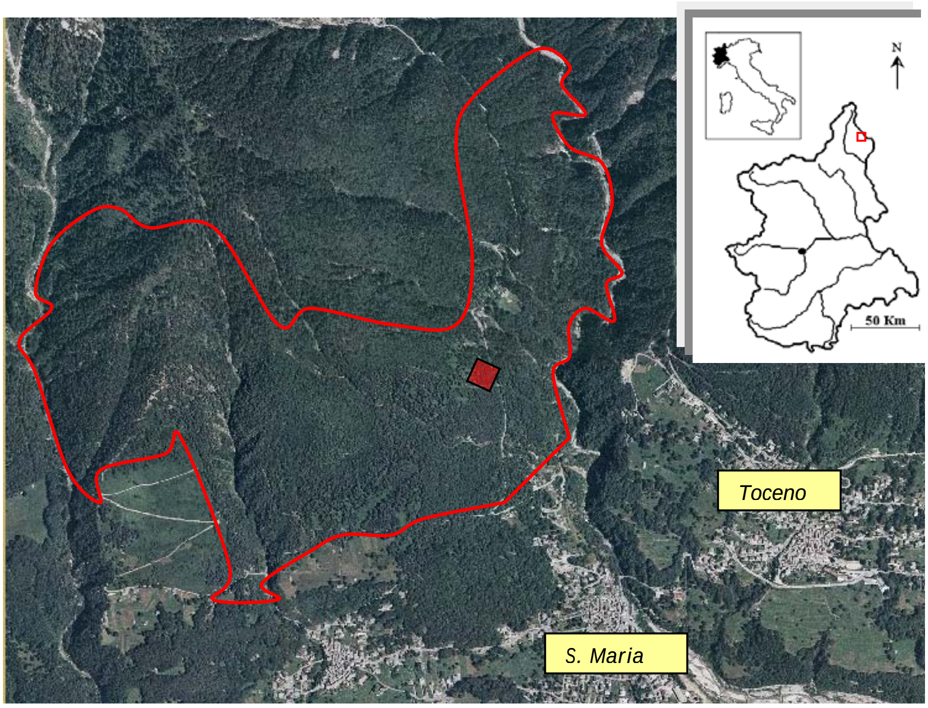

Figure 14 – Location of Scots pine stand in Santa Maria and positioning of the permanent sample plot.

First, the stand is positioned on the diagram according to current structural parameters. Dominant height forecasted by the diagram is quite close to the one measured in the field (see Table II.4). If coupled with site index curves, dominant height can be used throughout the diagram to assess current stand age (when unknown) and the time required by the stand to move on its projected development trajectory.

No site index curves were available for the study area. To infer site index, we used yield tables for Scots pine in Austria (Marschall, 1976); we assumed that the wide assortment of site productivities modeled therein grants their applicability in all site conditions implied by this study. Growth curves [Figure 15] indicate a fast initial growth followed by reduced height increment from age

80 on and a slowdown, a common pattern in early-seral species. Even on the most fertile sites, height growth curve finally flattens down; total height hardly reaches 35 m. Mean age at an height of 50 cm as measured by woody cores (Saponeri, 2006) would place this stand on the second-from-highest fertility class (SI = 30)[3], but because of a higher oceanicity than average climatic conditions underlying Marschall's tables we will place it in the best class (SI = 33).

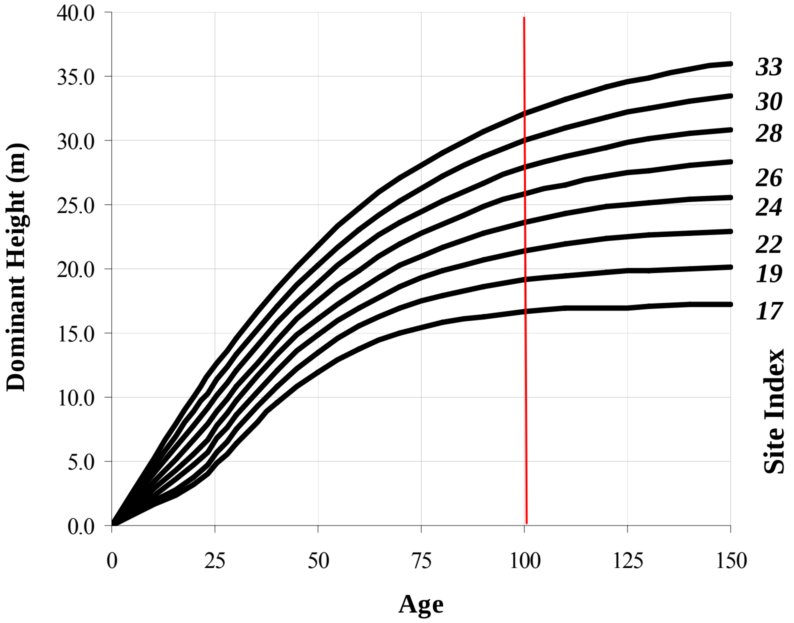

Figure 15 – Site index curves used in this study (adapted from Marschall, 1976). Base age is 100 years. Model form and statistical significance indices were not included in the yield tables.

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[3] It can take Scots pine seedlings up to 12 years to reach 50 cm height in dry climates (Gonzalez and Bravo, 2001) but this is not the case for the analyzed site, where because of the higher precipitation-related fertility pine seedlings are believed to reach an height of 50 cm in about 5 years. Total stand age therefore is 40+5 = 45 years.

The second step involves deciding target stand structure at the end of rotation. Most of the Scots pine harvested in Italy is used for packaging material; self-established stands are often located on poor sites, and the result is reduced growth rates and low stem quality (Dotta and Motta, 2000). Nevertheless, on fertile sites it is possible to attain size and quality classes suitable for timber use. The target QMD for this stand can therefore be set to 35 cm, i.e., an appropriate size for saw timber (CEN, 1997). Besides target size, the timber production goal can be translated into other silvicultural objectives, e.g., maximizing final yield, improving wood quality (small knots, maximum clearwood), or minimizing the time required to get at the end of rotation (EOR). We assessed the effectiveness of three silvicultural alternatives for pursuing one or all of the described goals: a) no intervention (the stand is left to natural growth following mortality dynamics); b) early thinning regime, planning just one strong selection thinning at an early stage of stand development in order to minimize logging costs; c) repeated thinning regime, planning more entries (low thinning) at fixed time intervals, in order to maximize net volume harvested. Management regimes are plotted on Figure 16.

According to the diagram [Figure 16A], the stand is already experiencing competition-induced mortality. Evidence of ongoing self-thinning dynamics has been found in the field, specifically the number of standing dead trees, the spatial pattern of surviving trees, the shape of dbh distribution and the mean live crown ratio (Vacchiano, 2007c).

The dotted line in the diagram represents a first approximation of the survivorship curve for the stand ("dynamic self-thinning line" according to Weller, 1990), i.e., its forecasted trajectory in the absence of silvicultural entries. In the early years, when average tree size is small and there is no mortality due to self-thinning, these survivorship lines track vertically, parallel to the Y-axis. The stand will continue to develop and grow without self-thinning mortality until it approaches the ZICM line. Once each stand passes this ZICM line, self-thinning will begin to occur and the density of living trees will decrease. This is illustrated on the diagram by the leftward trajectory of the survivorship line as it transects the ZICM line. As the stands continue to grow, more trees will die as each stand indefinitely approaches the 1.0 RD line. At a point close to 80% of maximum SDI (Long and Shaw, 2005), natural stands reach their maximum size-density relationship i.e., the biological carrying capacity of the site has been attained. Self-thinning mortality will continue within each stand as mean tree size increases. As a result, the survivorship line for each stand will continue to track leftward for the rest of its life, below and more or less parallel to the 1.0 RD line (Long and Smith, 1984; Archibald and Bowling, 1995). Some authors effectively tracked forecasted mortality curves for individual on the DMD, thus helping the projection of stand density and average size across time (e.g., Farnden, 1996). Without such trajectories, the DMD can not tell anything about the past history of the stand, which may be the result of natural self-thinning as well as the outcome of a recent disturbance by man or other agents.

The no-treatment option is the least costly and maximizes final yield; the main drawbacks are represented by the long rotation needed to attain merchantable size and by the fact that some part of total growth is lost due to tree death. The stand will undergo for a long time an intense competition, with slowed tree growth (hence the 160 years required to reach target size), short and compact crowns and closed canopy. Wood quality may benefit from the slow growth rate (Wichmann, 2002), but leaving the trees for such a long time in the stand means exposing them to a higher risk of damage due to biotic or abiotic disturbances, so that even very high yields may be hampered by low timber quality. Moreover, individuals grown in a highly competitive environment usually suffer reduced individual vigor, which may further aggravate the negative impact of disturbance agents.

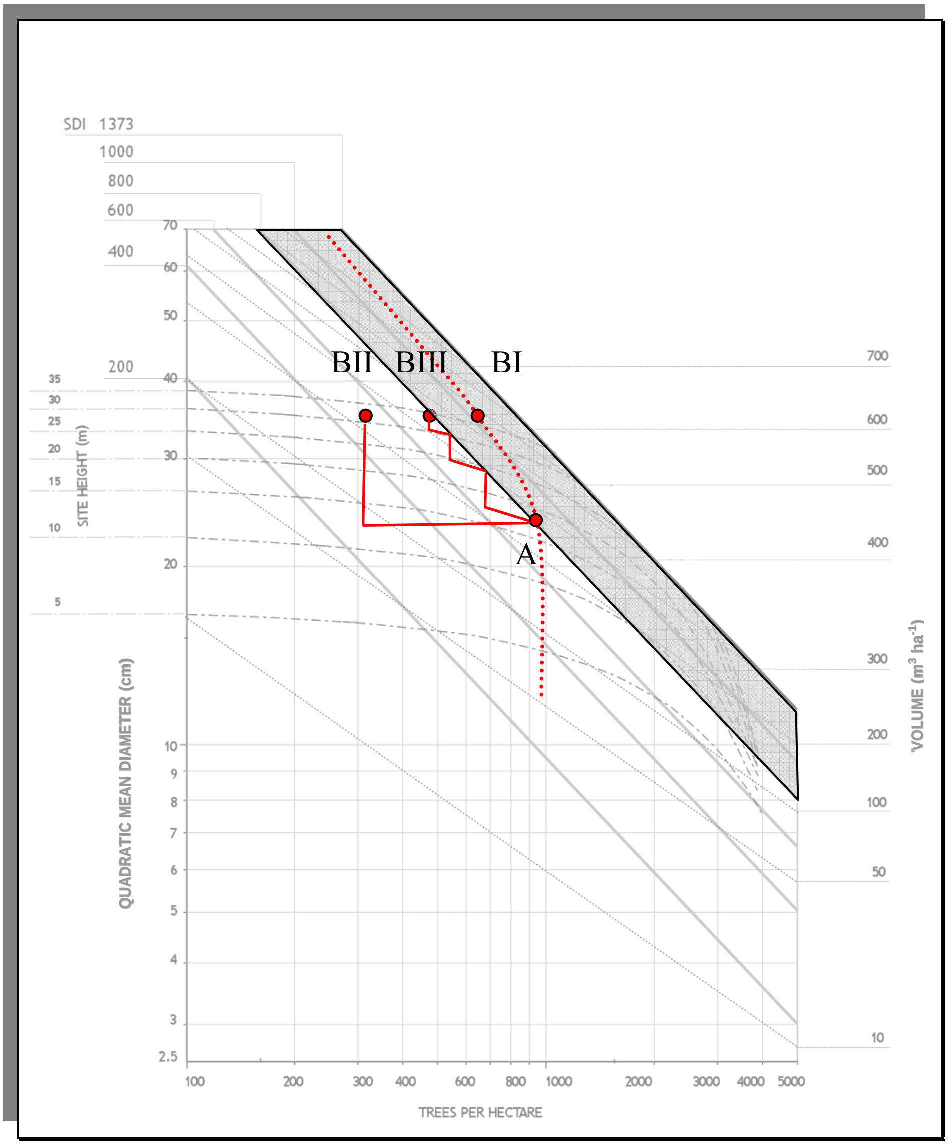

Figure 16 – Silvicultural alternatives for a Scots pine stand. A: initial stand; B: end-of-rotation target stand. i) No intervention (predicted trajectory of stand survival); ii) Early thinning; iii) Repeated thinning. Zone of imminent competition mortality (ZICM) is grayed out.

A feasible alternative would be devising a number of intermediate thinnings to reach target mean size without mortality losses, stimulate the expression of individual growth and regulate stand structure in order to avoid stem slenderness rates which may hamper mechanical stability. Trees growing in very dense stands develop a height-to-diameter ratio higher than open-grown trees; slenderness coefficients higher than 80 can be dangerous for individual tree an whole stand stability against snow or windthrow hazards (Dotta and Motta, 2000; Mitchell, 2000; Regione Valle d'Aosta and Regione Piemonte, 2006). A slenderness boundary may be represented on the DMD, substituting for the Height term in equation [3]; Figure 17 shows the region with H/D ratio >80 plotted on the diagram.

Alternative no. 2 develops around a single thinning, to be carried out at present with a strong selective criterion. This way, the stand is immediately released from competition and prepared for rapid growth of few, selected crop trees. Thinning from above has been suggested as a worthwhile practice in fertile Scots pine stands, since it provides high amounts of large logs. Selection thinning has also been found a better alternative if compared with low thinnings, whose weak selective power may well be carried out just by natural selection between young saplings, without the need for further intervention (Favetta, 1996). The proposed action involves reducing stem number to 300 trees per hectare, representing end-of-rotation density; the operation removes a volume of 200 m^3 ha^{-1}, which can be sold for small woodwork and packaging uses, and reduces QMD and dominant height, since it acts on the upper canopy layers.

The slenderness coefficient is kept on safe values for a longer time span; keeping total density low may help in promoting high crown vigor, granting a ready response to thinning treatment and future disturbances. We suggest choosing thinning intensity in order to attain target canopy cover, as determined from available data (see Figure 10; SDI higher than 200 may already determine a 70% crown cover) or from allometric relationships. Computing Hasenauer's (1997) dimensional equations for open-grown trees on local tree measurements, we computed 100% cover may be achieved with SDIs ranging from 190 to 320.

Rapid individual growth is the consequence of the strong decrease in competition intensity [Figure 18]. This results is obtained at the expenses of total yield, which suffers some reduction with respect to the previous case, even if the stand can get much earlier to the end of rotation. As a further alternative, we propose a traditional low thinning regime, devising three entries to reach a final density of 470 trees per hectare at target QMD. Target density is chosen so as to capture the most part of stand growth, without allowing mortality to set on. Therefore, target stand lies on the lower boundary of the ZICM, representing the upper management boundary ("constant lower limit SDI"); the lower management boundary is chosen in order to allow the development of a minimum mean live crown ratio of 0.4, i.e., the stand is entered when RD reaches 0.5 (see Figure 11). Thus, minimum tree vigor is guaranteed (Long, 1985; Smith, 1986) and promotion of competition-induced self-pruning and subsequent smaller branch size is achieved (Farnden, 1996). Once determined the boundaries of the so-called active management zone (McCarter and Long, 1986), the desired stand trajectory is worked backwards from target to current conditions. Stand trajectory during the thinning parallels the dominant height isolines, since low thinning remove only the smallest, overtopped individuals, thus increasing QMD at the same time. Timely and repeated thinnings (the fixed time interval reported in the table is just an outcome of site index-related age estimation) have the advantage of maintaining near constant crown closure throughout the rotation, mitigating the impact of logging activities on advance regeneration, and preserving slender trees from sudden isolation. The main drawback is the high operation cost, due both to low quality intermediate removal material and to the need for repeated entries. Total removals sum up to an intermediate yield between the previous alternatives, and so does rotation age (130 years). Timber removals (only obtained at rotation age) are less than the self-thinning regime, but twice the ones resulting from the early thinning regime.

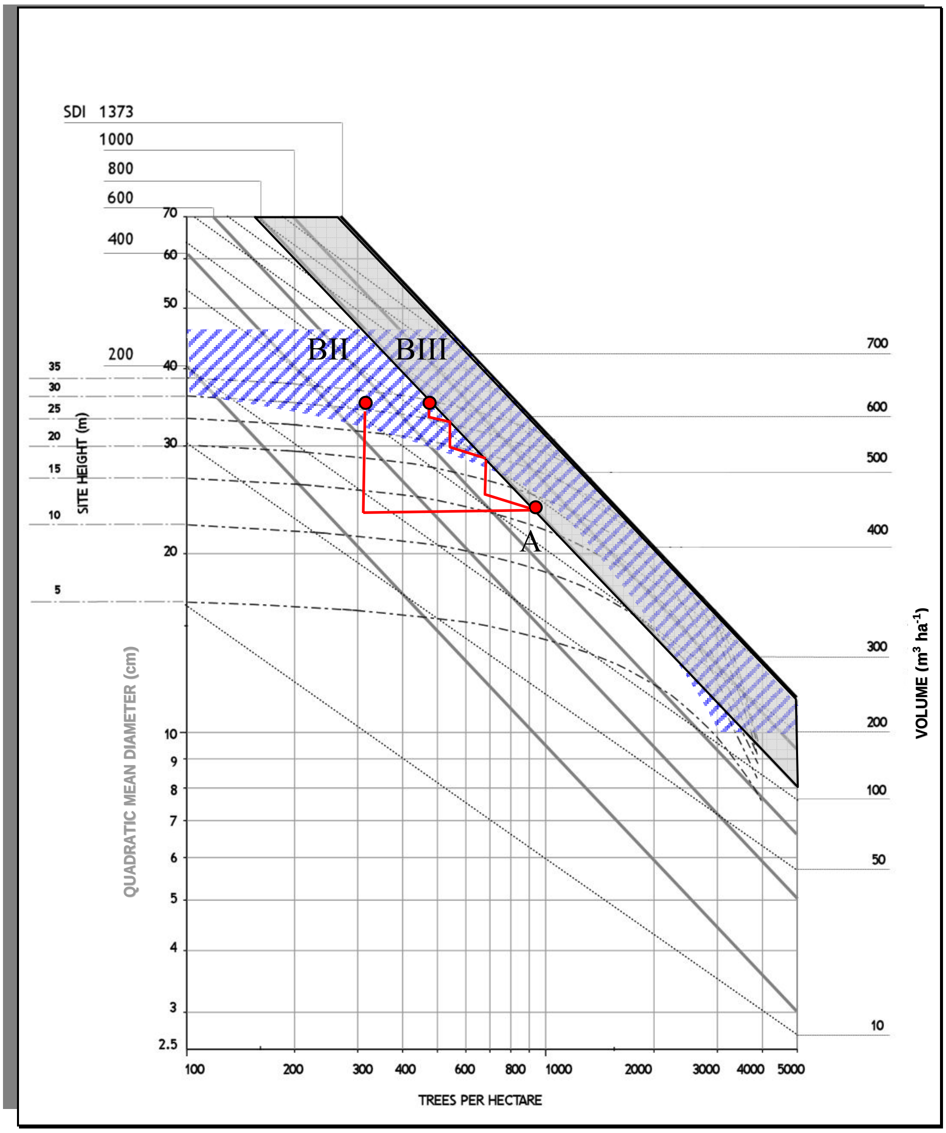

Figure 17 – Silvicultural alternatives ii and iii. Cross-hatching highlights possible stand developments characterized by high slenderness coefficients (H/D ratio >80).

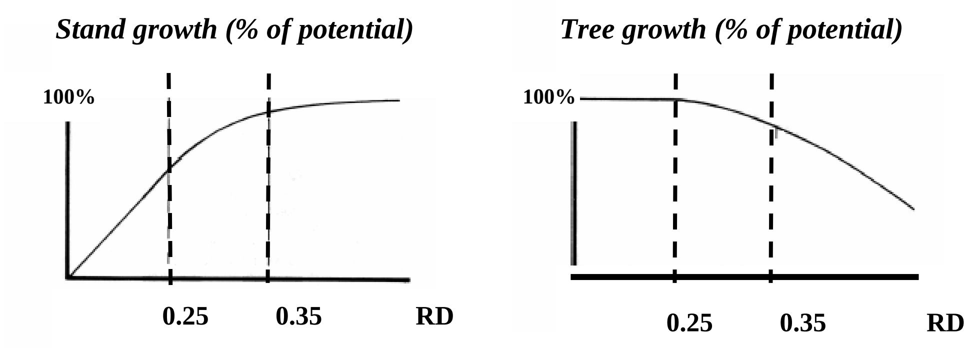

Figure 18 – Current annual stand and individual tree growth as related to growing stock. % SDI is the actual SDI expressed as a percent of the species' maximum SDI (from Long, 1985).

The parameters for the described density management regimes are reported in Table II.5. The active management options allow to attain the following silvicultural goals, as compared to the no-treatment option: shortening rotation length (BII and BIII), time gain to EOR, i.e., harvesting the biggest trees as soon as possible ("sudden sawlog", BII) and average to good wood quality (BIII as compared to BII; small knots, maximum clearwood). Management regimes can be planned at any intermediate level between the described alternatives; criteria for deciding target average size and bounding the active management zone may include attaining minimum merchantable size, observing critical time for thinning operations or minimum times for re-entry, maintaining full site occupancy (Anta and Gonzalez, 2005), or other requirements related to non-timber forest values (e.g., habitat features, fire or pest risk, understory development, etc.) (Smith and Long, 1987; McTague and Patton, 1989; Lilieholm et al., 1993; Sturtevant et al., 1996; Hayes et al., 1997; Bailey and Tappeiner, 1998; Mitchell, 2000; Shaw and Long, in press).

	Age	H_{dom} [m]	N_{before}	N_{after}	QMD_{before} [cm]	QMD_{after} [cm]	$V_{removed}$ [m^3 ha^{-1}]
Starting conditions	***45***	**17**	**950**		**24**		
i) Final harvest	*160**	37	660		35		492
Total yield							*492*
MAI							*3.1*
ii) LT1	*45*	17	950	700	24	25	50
ii) LT2	*60*	25	700	550	28	30	30
ii) LT3	*85*	31	550	470	32	33	40
ii) Final harvest	*130*	35	470		35		360
Total yield							*480*
MAI							*3.7*
iii) ST	*45*	17	950	300	24	23	200
iii) Final harvest	*100*	33	300		35		240
Total yield							*440*
MAI							*4.4*

Table II.5 – Comparison of the three density management alternatives. Stand parameters before and after silvicultural entry, volume removed per entry and total yield at and of rotation. Mean annual increment (MAI) is computed from total yield and rotation age.

**Projected dominant height is out of the bounds imposed by site indices; real height will flatten out as age increases*

Currently recommended density management regimes for Scots pine on the Alps (Dotta and Motta, 2000; Del Favero, 2004) forecast lower end-of rotation yields if compared with DMD predictions, i.e., 150 to 350 m^3 ha^{-1}. Camerano et al. (2005) reference a mean yield of 210 m^3 ha^{-1} for the area under study. Nonetheless, such figures are associated to shorter rotations. Traditional silvicultural regimes in Piedmont seldom last more than 80 years for Scots pine, even if rotations tend now to get longer (up to 120 years, much like in other Italian alpine regions) (Ott et al., 1997; Del Favero, 2004). As previously noted, fertility does not influence the trajectory of developing stands, but only the time required to complete it. Del Favero (2004) suggests a density of 1200 to 1600 trees per hectare at age 40 for natural stands in the Alps, a time when competition-related mortality starts to occur (Suchecki, 1947). This corresponds to fertility classes laying in the lower part of the site index diagram used in this study. If undisturbed, an average to low-fertility stand (a common situation in mountain areas of the Alps) would reach according to the diagram a final yield of 300 m^3 ha^{-1} with a QMD of 25 cm after 80 years (SI = 22).

Moreover, the referenced yields do not take into account removals from intermediate thinnings. Even if these are seldom executed, either because of high costs or to obtain good-quality wood with narrow growth rings (Bernetti, 1995), their implementation is recommended for fertile sites, where they may provide merchantable-sized material. Advised planning strategies usually rely on low thinnings starting from age 40 (Del Favero, 2004), sometimes following a pre-commercial thinning at age 10-15 to accelerate stand growth.

Description of end-of-rotation stand structure and yield in alternatives ii) and iii) is not far away from literature recommendations, though projected rotation times are quite longer than expected. This can be due to the somewhat limited statistical significance of the key allometric relationships modeled herein, and particularly of the Top Height – Quadratic Mean Diameter curves, that imply rotation age as a direct consequence. The available inventory data forced us to use the height of the dominant tree on the plot (site trees) as a proxy for dominant height, but the estimator is obviously biased. This distortion has a strong effect both on the shape of H-D isolines, and on the accuracy of parameters describing target stand structure. Errors in age predictions may also be related to the unavailability of locally calibrated site indices; height growth models used may be biased towards generally poorer sites (i.e., more continental climate). We therefore consider the computation of local site index tables a high-priority task in order to achieve more accurate stand growth predictions.

In any case, dynamics modeled do not refer to any specific stand, but rather to the average structural and site features across a wide geographical range. The user can make use of different site index curves, but this may not be enough to reflect local variability, which in many cases is related to the peculiar past history of the stand. DMDs can give little, if any, information about past stand development; stands sharing the same position on the diagram may be characterized by very different structures, especially when felling or disturbances have previously occurred (e.g. higher or lower crown compactness, number of canopy layers, crown depth…) (Shaw and Long, in press).

DMDs have not been used to date in the calibration of logging intensity as a function of regeneration needs. There are numerous studies on levels of herb forage production rates under different relative densities (Moore and Deiter, 1992; Naumburg and DeWald, 1999). RD of the overstory can be manipulated to levels allowing the exploitation of the available growing space by the understory as well as by self-establishing regeneration of more or less tolerant species (i.e., RD lower than at full site occupancy). Scots pine stands in the Alps are usually naturally regenerated. Moreover, in most cases recently established pine forests are gradually undergoing successional dynamics driven by late-seral species colonization (Camerano et al., 2005). Even when this is not happening yet, facilitating succession is considered a major silvicultural goal, in order to enhance stand stability by a more diverse stand structure and promote natural dynamics (Dotta and Motta, 2000). DMDs are strictly built around monospecific communities, because the position of the self-thinning line and the estimate of overall growing space are species-specific parameter. Nevertheless, the implementation of regeneration models (Pukkala, 1987; Prévosto et al., 2003; Castro et al., 2004) capable of assessing growing space requirements for the species of interest could help in designing proper suitability zones within a species’ DMD.

Figure 19 represents a conceptual model for modeling establishment of a late-seral species under a Scots pine cover. Suitability zone boundaries are determined by a) relative density, b) Absolute density, c) Dominant height of the parent stand. A higher QMD is assumed to be associated with taller trees, which attenuates the effect of high canopy cover making more light available on ground level. Site fertility can be represented on the z-axis, in which case the suitability zone will be deformed according to higher or lower site attitude towards seedlings.

Figure 19 – Suitability zone for a supposed shade-tolerant species rejuvenating under a Scots pine cover. The model focuses on solar radiation niche.

However, the newly established stand poses the additional problem of computing new allometric relationships and a new self-thinning boundary, associated with increasing degrees of species and/or structural mixture. Self-thinning boundaries for mixtures have seldom been successfully addressed by ecological literature (Puettmann et al., 1992; Sterba and Monserud, 1993; Wilson et al., 1999; Torres-Rojo and Velázquez-Martínez, 2000; Solomon and Zhang, 2002). Definitive species are believed to self-thin according to higher limits than early-seral species, i.e., more individuals can coexist on a defined area (Westoby, 1984). The new self-thinning boundary could be modeled as a function of the degree of mixture in stand, its curvature being shaped according to the ecological characteristics of the two species [Figure 20].

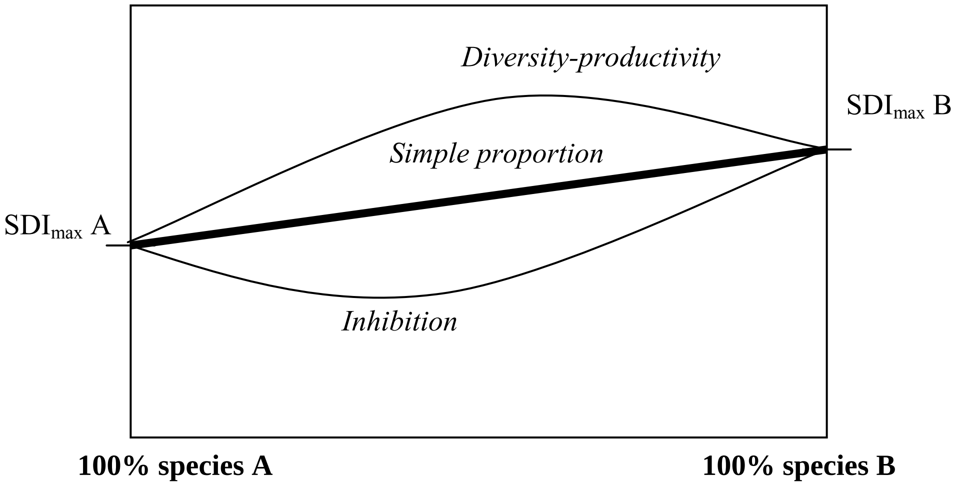

Figure 20 – Three possible scenarios for maximum self-thinning line in 2-species mixed stands, where SDI_{max} *is different for the two species. The first possibility is that* SDI_{max} *for the mixture is simply weighted by the proportion of the 2 species. This situation essentially assumes that the species with higher* SDI_{max} *will out-compete the other species locally, but that* SDI_{max} *for the stand is limited by the abundance of the more competitive species. The second possibility is that* SDI_{max} *will be highest at some mixture of the 2 species. This scenario is in keeping with the diversity-productivity hypothesis (e.g., Tilman et al. 1996; Porté and Bartelink, 2002), suggesting that the 2 species are not limited by a common resource, but are limited by different, non-overlapping resources. The third possibility is that* SDI_{max} *is lower for mixtures than for pure stands of either type. This appears to be the least likely possibility, but there may be cases where the species present both inhibit the site occupancy of the other (from Shaw, 2006).*

Case 2: Direct protective function

With increasing population density and pressure from emerging tourism in mountain environments, the protective function of the forests is becoming the primary forest function (Krauchi et al., 2000). Currently designated protection forests are mostly anthropogenically influenced secondary forests; 30% of Scots pine stands in the study area are designated as protective forests, 4,000 ha of which perform a direct protective function (Regione Valle d'Aosta and Regione Piemonte, 2006). The direct-protective function of a forest implies that the forest directly protects people, buildings and infrastructure against the impact of natural hazards such as snow avalanches and rockfall (Mayer and Ott, 1991; BUWAL, 1993; Berger and Renaud, 1994; Brang, 2001; Herold and Ulmer, 2001). Conditions promoting natural evolutionary processes and ecological stability in protection forests could be categorized in three general criteria (Motta and Haudemand, 2000; Dorren, 2003):

1. diverse composition of species;
2. sufficient natural regeneration;
3. optimal forest structure.

Several attempts have been made to describe structural features that best improve the protective function of a forest stand (Suda, 1989; Chauvin et al., 1994; Wasser and Frehner, 1996; Schönenberger, 2001; Vospernik, 2002; Frehner et al., 2005; Schwitter et al., 2006; Wehrli et al., 2006), depending on the kind of natural hazard against which protection is intended. Since most Scot pine stands are located on mid-elevation slopes, their protective action is most effective against rockfall, preventing triggering of the event in source areas, reducing kinetic energy of falling boulders in the transition zone and shortening distance traveled by rocks in accumulation areas (Jahn, 1989; Dorren et al., 2004, 2007). Proposed structural criteria maximizing protection from rockfall can be summarized as follows:

a. Minimum stand density: 300 to 400 trees per hectare (Wasser and Frehner, 1996);

b. Relative density: SDI 600-1000 to avoid both excessive openness of the stand and stability threats due to a high degree of crowding (Brandli and Herold, 2001);

c. Vertical structure: two-layered, sufficient viable trees in two different stages of development;

d. Horizontal structure: individual trees or small clusters. Crown cover less than 60% is considered a negative factor (Brandli and Herold, 2001);

e. Gaps in the stand: mean tree free distance (i.e., the average distance between two rock impacts) < 20-40 m (Gsteiger, 1989; Zinggeler, 1989; Frehner et al., 2005). The MTFD basically calculates the probable mean distance between two tree impacts in a forest stand; its concept was later adapted by Perret et al. (2004) and Dorren et al. (2005). According to Vospernik (2002),

[5] $$MTFD = \frac{A}{Nd_{rock} + \sum dbh}$$

where A is stand area [m^2],

d_{rock} is diameter of falling boulders [m],
N is stand density,
Σdbh is sum of tree dbh [m] (computed in this study by multiplying QMD by tree density).

f. Diameter distribution: mean stand diameter and diameter dispersion of a stand carry different weights according to the significant diameter of the falling rocks. Brandli and Herold (2001) recommended a “stand diameter” of ⅓ to ½ of target boulder diameter. Other parameters taken into considerations are the number of trees greater than a certain dbh (e.g., 12 or 16 cm) or the dbh range of stability supports (see after)[4];

g. Species composition: a minimum broadleaved component of 10 to 30% is advised in Scots pine stands (Regione Valle d’Aosta and Regione Piemonte, 2006), according to forest cover type and forecasted speed of stand dynamics;
h. Tree slenderness: H/D ratio lower than 70-80 (mean slenderness in the upper layer);
i. Tree crowns: very limited asymmetry, minimum crown ratio ranging from 0.3 to 0.5. Criteria h. and i. apply to “stability supports”, i.e., trees or cluster of trees supporting the stability of the stand (Wasser and Frehner, 1996).
j. Regeneration: more than 30 to 60% of available seedbed free from herbaceous species competition. 1-2 advance regeneration patches per hectare, diffuse to abundant seedlings on bare soil on a certain portion of stand area (1 to 75% according to forest cover type).

Brandli and Herold (2001) distinguish criteria valid to asses the current protective effect of the forest from those describing its sustainability on the long term (stand structure, diameter dispersion, tree slenderness and crowns, regeneration). Current stability standards can be used to determine a silvicultural minimum goal, i.e., stand structure allowing minimum acceptable

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[4] Further refinements of the dbh structural criteria are not treated in this study. Statistical tools have been proposed in literature in order to represent dbh distribution-related requirements on the diagram, i.e., target dbh frequency (Shaw and Long, in press) or size heterogeneity (Vospernik, 2002). The optimal combination of stand density and mean dbh, however, depends on the size and energy of the falling rock. Currently, the notion of rock size dependent forest stand management has been integrated in new guidelines (Frehner et al., 2005; Gauquelin et al. 2006).

reduction of the hazard, and can be represented on the DMD space [Figure 21]. Transition from non-effective to fully functional zones can be smoothed assigning weights proportional to the protective effect associated with different values of the structural parameters under consideration; each functionality zone can be characterized by a synthetic index of direct protection which is the sum of such weights (Motta and Haudemand, 2000).

Figure 21 shows as a case study a protective Scots pine stands and its projected development. The stand is located in the municipality of Antey St. André (UTM: 391 338 E, 5 072 993 N) on an elevation of 1200 m a.s.l. A permanent sample plot (100x80 m) has been established in the transition zone of a rockfall-prone slope [Figure 22], where the stand was designated as part of a direct protection forest (Regione Valle d'Aosta and Regione Piemonte, 2006). Across the whole stand (surface: 24 ha), stand density is 288 trees ha^{-1} and Scots pine standing volume amounts to 132 m^{3} ha^{-1}. Figure 22 also shows tree size class distribution of the sample plot; Scots pine represents 83% of the trees, with a QMD of 22.7 cm and an overall density of 1039 trees ha^{-1} (dbh >7.5 cm). Mean live crown ratio is 0.4; overall canopy cover in the plot is 51%, due to sparse gaps located on recent scree slopes. Reported age for the oldest trees is 160 years; if Marschall's site index tables are assumed to hold true, fertility class may be as low as SI=19 m.

Apart from canopy cover, the stand satisfies all the other criteria for current protective function (including a roughly bimodal size class distribution) and is therefore located in zone I in the DMD. Nevertheless, a look at mortality trajectories, which we assume to begin sooner and take place at a higher rate than in undisturbed stands because of the negative impact of the rockfall-induced disturbance (Vospernik, 2002), advises us to act with prompt silvicultural measures in order to avoid deterioration of the protective effect of the forest. Natural development will soon lead the stand first in the lower functional class, then in the non-effective area (zones 3 and 4 according to Motta and Haudemand, 2000).

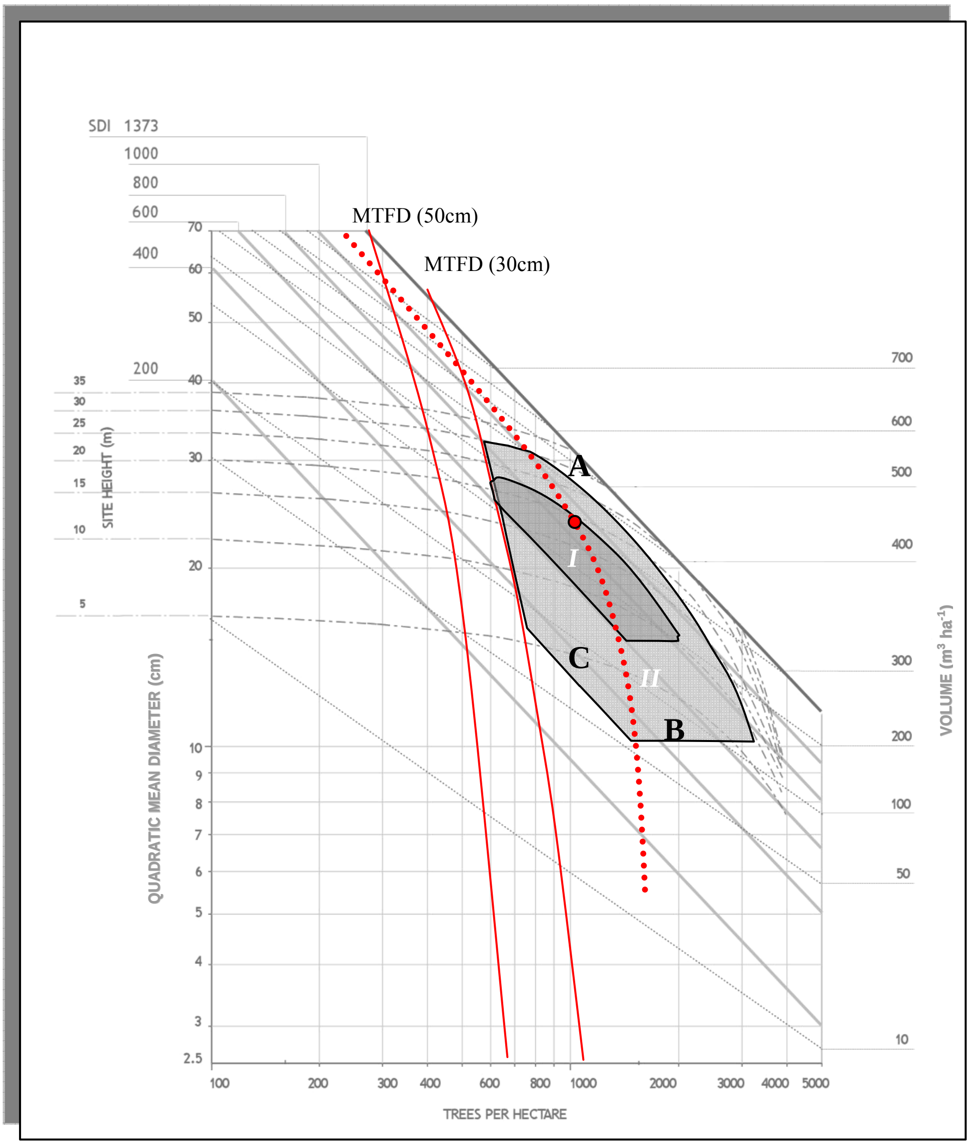

Figure 21 – Suitability zones for current direct-protective function of Scots pine stands on DMD space. Simplified weighting scheme with a two-value scale: zone I (core, optimal protection) and zone II (minimum acceptable protection), according to Motta and Haudemand (2000). Boundary of the zones are defined by: A) slenderness: (H/D ratio lower than 80 and 90 respectively (criterion h.), B) minimum tree dbh: ½ and ⅓ of target boulder diameter (here 30 cm, criterion f.), C) minimum canopy cover: crown closure >60% as computed according to Long (1985), i.e. RD=0.25, or calculated from data [see Figure

9], i.e., RD=0.44, in the most conservative option (criterion d.). Red continuous lines represent thresholds for MTFD = 30 m (rock diameter: 30 and 50 cm, criterion e.) according to equation [5]. Mean live crown ratio is assumed to be higher than 0.3, at least for stability supports (i.e., dominant trees) throughout zones I and II (criterion i.). Criteria based on SDI ranges are not represented here, since we assume other threshold to account already for effective size-density combinations.

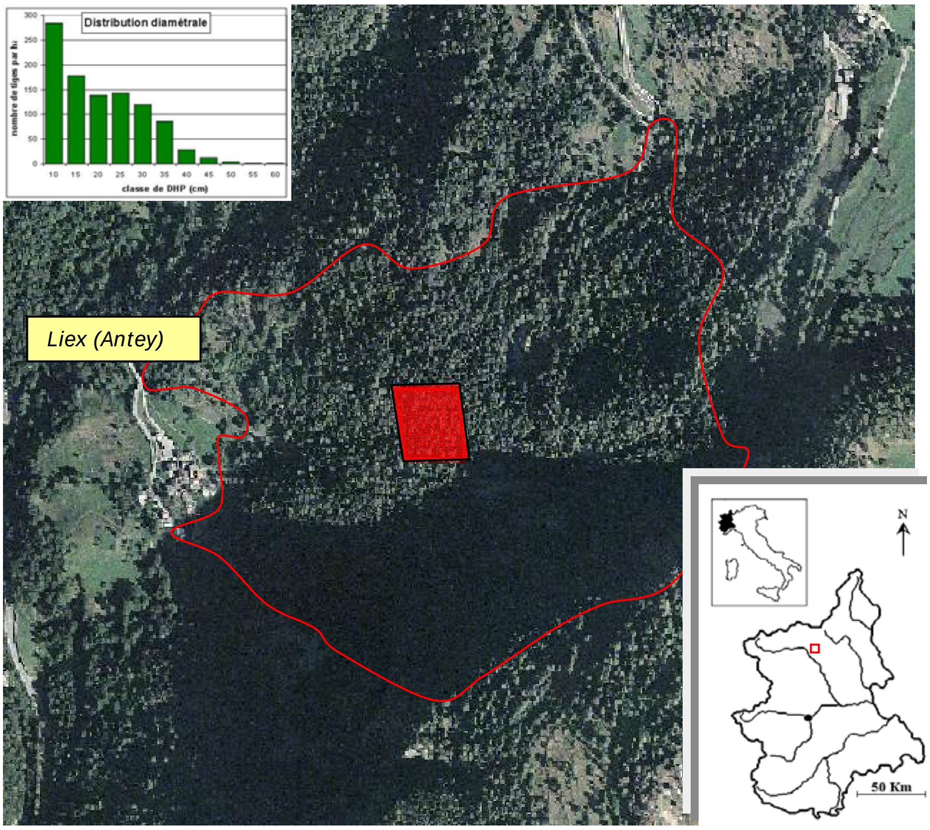

Figure 22 – Location of Scots pine stand in Antey St. André and positioning of the permanent sample plot.

Silvicultural guidelines recommend for this stand a group thinning, aimed at removing unstable elements, releasing stability supports from competition and stimulate growth and regeneration of the broadleaved component. A rapid assessment of the DMD reveals the effectiveness of such a choice: a light selective thinning around the most stable trees would push the stand back on a lower competition status, reducing the risk of early breakdown and making additional growing space available for broadleaves (downy oak and chestnut), that are highly effective in the rockfall transition zone. Pushing the stand into zone II (representing here the active management zone) might be the best choice if the higher rockfall hazard due to reduced density and crown cover was relieved by support measures such as temporary wooden fences or lying logs.

Sustainability standards deal with a long-term view of stand development that transcends the scope of tools intended for one-rotation planning. Management of protective forests is a complex task (Brang et al., 2002) aimed at maintaining stand stability not only preserving it from disturbance-induced breakdowns, but also providing it with a high resilience, i.e., the power to quickly recover an efficient structure once it has been hampered by adverse events (Grimm and Wissel, 1997; Motta and Haudemand, 2000). Instability problems may be simply caused by overmaturity if silvicultural interventions are absent, as it is impossible to stop the evolution of a forest. Therefore, silvicultural measures must be aimed at guaranteeing continuity of the protective function across most stages of development. Ideally, a forest ecosystem that fulfills the three general criteria mentioned above enters a steady state in which small patches with alternating developmental phases provide a collective stability for the stand or forest, which is sub optimal for protection on the short term, but as optimal as possible on the long term (Dorren et al., 2004). The most stable forest structure is a small-scale mosaic of all classes of tree size and age (Ott et al., 1997; Krauchi et al., 2000; Motta and Haudemand, 2000).

DMDs can be used not only to assess the current protective effect of a forest (see Figure 21), but also to plan management actions needed both to improve current protection and to ensure its sustainability over time. DMDs are intended to model even-aged stands or cohorts belonging to the same management unit. Several of these charts can be built up and combined to monitor and forecast the development of the aforementioned structural mosaic, anticipating the impact of managing actions and disturbances on the different structures simultaneously present on the field.

Case study 3: interactions with natural disturbances

The reciprocal interaction between competitive dynamics and disturbance regimes has not been thoroughly examined to date, especially in the Alpine region. On a long-term scale, disturbance patterns are well known to be responsible for changes in stand structure and species composition, triggering successional events (Frelich, 2002); only a few authors focused on the stability of growth and competitive relationships when disturbances are acting at different scales (Clark, 1992; Guo and Rundel, 1998; Wirth et al., 1999).

Self-thinning and disturbance-induced mortality have been studied as isolated processes. The mortality patterns they determine have opposite characteristics (i.e., spatial distribution, target tree size, density-dependence), therefore simultaneous modeling is a difficult task. Nevertheless, they also present large overlaps: some disturbance types are strongly density-dependent (e.g., pest outbreaks, root rot, windthrow), and all off them generate deviations in the mortality curve of stands they disturb. Such deviations may take place only during some developmental stage, e.g., mature stands representing a transition between the two patterns of mortality as pests, pathogens, and wind gradually become more important than competition (Franklin et al., 2002). Stressed stands will suffer reduced growth rates [Table II.6], determining a slowed speed of development, and experiment a higher mortality, with the effect of being scattered well below the upper thinning boundary (Guo and Rundel, 1998).

Disturbance type	***BAI loss %***	***Reference***
Rockfall	1.18	Dorren and Berger (2006)
Butt rot	0.73 - 1.85	Hellgren and Stenlid (1995)
Peeling	1.42	Schimitschek (1939)
Defoliation 30-40%	3.36 - 4.36	Rohle and Schmidt (1987), cited in Vospernik (2002)

Table II.6 – Annual basal area increment reduction to Norway spruce forest stands caused by different disturbances (from Vospernik, 2002).

When disturbances happen according to patterned regimes with predictable intensity and return interval, their influence on mortality dynamics may be systematically evaluated by depicting modified competition boundaries for stands under a particular disturbance regime (Wirth et al., 1999).

This requires systematic inventories undertaken over large spatial and temporal extents. Even when this is not possible, DMDs can be useful in determine a stand's proneness to a certain disturbance (static approach). Different "proneness zones" can be plotted down according to criteria maximizing the risk of the actual impact of specific disturbance types (e.g., *Bark beetles*: Anhold et al., 1996; Perkins and Roberts, 2003; *Pine shoot beetle*: Cedervind et al., 2003; *Fuel assessment*: Cruz et al., 2003; Reinhardt and Crookston, 2003; *Windthrow*: Mitchell, 2000; Cucchi et al., 2005). The delineation of high-risk zones can be coupled with silvicultural planning, so as to investigate the consequences of thinning and logging operations on stand stability and health status.

Finally, DMDs can help in assessing future development of residual stands after single or repeated disturbance hit (dynamic approach). The effects of an additional growing space suddenly made available, and the changes in average size and density can be modeled just like silvicultural operations. Residual stands can thus be plotted in their projected trajectory through the different developmental stages, accorded they can be managed as single units and the disturbance impact be uniform throughout all the analyzed area (for an application of this, see Shaw, 2002). Further exposure to disturbances may be modeled either superimposing more than one size/density reduction on the diagram, or modifying the basic allometry and stand dynamics, in order to adjust mortality rates to the foreseeable disturbance regime. This will be the subject of subsequent studies to be accomplished on Scots pine in the Alps.

Conclusion

DMDs proved valuable tools for assessing stand structural conditions, forecasting future stand development, comparing the effectiveness of different silvicultural management strategies, and modeling the impact of exogenous dynamics and the response of the stands to scenarios of future change. We think that a DMD for Scots pine in the Alps will provide knowledge about stand structural dynamics to be expected as a consequence of several management operations. When integrated with estimates of structural stages best suited to fulfill desired forest functions, the diagram can aid in the comparison of species-specific management scenarios and this represents a valuable tool for sustainable management of the pine resource.

The case studies proposed in this study help in showing how the DMD can be effectively applied, even in the field, to plan management operations aimed at maximizing timber revenues or other non-productive functions of pine stands, like in the identification of priorities for thinning protective stands.

Like other models, DMDs should always be applied using the best local knowledge and silvicultural insight. The model proposed in this study still suffers from limitations related to its usability in heterogeneous structures or sites, even if Scots pine stands in the study area tend to attain fairly regular structural stages. The poor significance of model functions, due to limited data availability, suggests the need of additional sampling to validate the allometric relationships that represent the “backbone” of the diagram, and eventually, the importance of a properly designed inventory for future extension of the diagram to other forest species. Nevertheless, the use of forest inventories based on different spatio-temporal scales is a key to examine ecological dynamics at multiple levels and test the validity of management indications by means of long-term monitoring research.

Chapter III: Competition at the stand and tree scale in Scots pine (*Pinus sylvestris* L.) forests of Northwestern Italy[5]

Introduction

Competition among trees is an interaction between individuals, brought about by a shared requirement for a resource in limited supply (i.e., its availability is lower than the level that guarantees optimal growth of the individuals) and leading to a reduction of the performance of at least some of the competing individuals (Kimmins, 1987; Brand and Magnussen, 1988; Begon et al., 1996). The resources involved and their absolute availability may include light, water, nutrients, and physical growing space (Daniels et al., 1986). Competition has long been known as a primary process governing individual plant growth rate, population size, community structure, diversity and development (Harper, 1977; Grime, 1979; Weiner, 1986; Shainsky and Radosevich, 1992; Oliver and Larson, 1996; Newton and Jolliffe, 1998; Simard and Sachs, 2004; Simard and Zimonick, 2005).

Competition has several attributes, and it can be examined from different perspectives, including: importance, intensity, effect, response and outcome (Gibson et al., 1999; Connolly et al., 2001; Sackville Hamilton, 2001). The intensity of competition is defined as the amount by which competition reduces the optimal condition of an individual, while the importance of competition is the degree to which competition contributes to the overall decrease in fitness relative to other processes affecting the performance of the organism (Welden and Slauson, 1986). In exploring the effect of competition, researchers evaluate how competition by companions influences target plants, while the response to

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[5] Based upon Vacchiano G., Lingua E., Motta R. (2006), *Pinus sylvestris L. forests in western Italian Alps: competition dynamics and canopy structure*, proceedings of SAF National meeting, Fort Worth, October 19-23, 2005, 15 pp. [CD_ROM].

competition entails the ability of target plants to avoid being suppressed by their neighbors (Goldberg and Werner, 1983; Goldberg and Fleetwood, 1987). Finally, the outcome of competition refers to the role of competition in directing long-term adjustments in species composition and structure, i.e., it pertains to the determination of which individuals or species “win” and “lose” as a result of competition.

Forest ecologists typically have approached the study of the competitive effects of adult trees through one of two alternate approaches. The more mechanistic one has been to focus on competition for a particular resource exploring (1) the effects of trees on the availability of the resource (i.e., light extinction by tree canopies, e.g., Canham et al., 1994) and (2) the responses of individuals to the altered availability of the resource (e.g., Pacala et al., 1994; Kobe et al., 1995). A more phenomenological and more widely applied approach has been to use regression analysis of the growth and survival of individuals as a function of the distribution, size and abundance of neighbors (e.g., Newnham and Smith, 1964; Bella, 1971; Lorimer, 1983; Biging and Dobbertin, 1992, 1995; Wagner and Radosevich, 1998; He and Duncan, 2000; Canham et al., 2004; Uriarte et al., 2004).

The mechanistic link between the abundance, size, and spatial distribution of neighboring trees and the strength of both aboveground and belowground competition can be represented by mathematical expressions called competition indices (CI). CIs attempt to quantify in a simple figure the effects of neighboring plants on the growth of an individual tree (Vanclay, 1992). Stand-level competition indices reflect the degree of tree crowding per unit area (Husch et al., 1982), allowing to compare stand development in stands with different competitive status (Hynynen and Ojansuu, 2003). Individual-based CIs reflect the local density of competitors interacting with an individual tree (Tomé and Burkhart, 1989). They quantitatively assess the intensity of competition experienced by focal trees and allow to quantify the influence of neighboring individuals on the growth of the subjects (Hynynen and Ojansuu, 2003), on both an individual and an average stand scale. They may be distance dependent, if they rely on tree location, and distance independent, if using only subject tree attributes and stand-level estimates of density (Biging and Dobbertin, 1992, 1995).

By aggregating several different measures, indices can express and quantify composite ideas that may better characterize competition than what is possible through a simple primary measure (Hunt, 1982). By condensing and organizing experimental results indices can help researchers interpret complex data, and the use of the same index by different researchers may help results from different studies to be compared.

The interpretation of the outcome of competition can depend critically on the way competition is measured (Freckleton and Watkinson, 1999). Several reviews of competition indices are available in literature (Mead, 1979; West, 1983; Aarssen, 1985; Connolly, 1986, 1987; Wilson, 1988; Rejmanek et al., 1989; Snaydon, 1991; Grace et al., 1992; Cousens and O'Neill, 1993; Grace, 1995; Garnier et al., 1997; Jolliffe, 1997, 2000; Loreau, 1998; Goldberg et al., 1999; Jolliffe and Wanjau, 1999; Sackville Hamilton, 2001, Weigelt and Jolliffe, 2003). Past studies showed that no index is universally valid, different indices performing better with different species and ecological situation (e.g., Biging and Dobbertin, 1995; Larocque, 2002). Investigations into the performance of spatial-explicit competition indices (Opie, 1968; Alemdag, 1978; Lorimer, 1983; Martin and Ek, 1984; Daniels et al., 1986; Pukkala and Kolstrom, 1987; Tomé and Burkhart, 1989; Biging and Dobbertin, 1992; Wimberly and Bare, 1996; Bachmann, 1998; Soares and Tomé, 1999; Miina and Pukkala, 2000; Stoll and Weiner, 2000; Mailly et al., 2003; Corral Rivas et al., 2005; Canham et al., 2006), found that the inclusion of spatial information often provided little extra improvement of efficiency. On the other hand, most of the authors also reported their preference for particular indices, i.e., the ones that seemed to perform the best compared to empirical data, but there is no general agreement on the indices preferred. Still, various spatially explicit competition indices have been included in growth models and forest simulators (Pacala et al., 1996; Kahn and Pretzsch, 1997; Bachmann, 1998; Pukkala et al., 1998; Vettenranta, 1999; Courbaud et al., 2001; Moravie and Robert, 2003; Vanclay, 2006)

Plant community structure can be though of as having six components: composition, size distribution, age distribution, spatial distribution, density and history. Each of the components can be informative and indicate the likely processes that influence that structure (Larsen and Bliss, 1998). Spatio-temporal processes involve the development of spatial patterns over time, thus providing a link between pattern and process in plant communities, and playing a crucial role in understanding ecosystem dynamics. Analysis of local spatio-temporal stand dynamics in selected areas may provide useful information about the future development of Scots pine stands, and about the effects triggered by differences in land-use history, climatic factors and exogenous disturbances on stand growth, mortality and succession. Research of a competition measure effectively representative of stand dynamics would have positive drawbacks on the modeling of future stand development. Simulation of individual-scale processes is needed not only to forecast growth and survival of single trees, but also to assess growth and mortality-related stand dynamics and extrapolate the quality of their interrelationship with environmental factors (Brang et al., 2002). Moreover, individual-based modeling allows to overcome the limitations imposed on large-scale modeling by local differences in stand structures (Monserud and Sterba, 1996).

The aims of this study are: a) to assess the intensity of competition in selected Scots pine stands differing for history, site characteristics and disturbance regime; b) to reconstruct past development of the stands from the establishment phase on; c) to evaluate the effect of current competition on tree growth and survival; d) to identify the best competition index and the most informative tree variables for evaluating influencing competitive relationships, for their upcoming inclusion in a basal area growth model.

Current structure and competition dynamics were analyzed in their response to stand history. The establishment phase, successive tree development and anthropogenic disturbance factors were reconstructed by recurring both to historical archives (documental descriptions and acts, old forest management plans) and to biological archives from dendrochronological studies, pursuing the integration of independent sources of analysis (Swetnam et al., 1999).

Methods

Field measurements

A total of 8 permanent sample plots (70x70 m) were established in the summer of 2005; Table III.1 summarizes the main site descriptors for the study areas. Plots are representative of the different communities Scots pine forms in the western part of Italian Alps (Camerano et al., 2004; Vacchiano, 2007a); a descriptive summary of the plots is enclosed in the Results paragraph.

All standing live and dead trees (dbh > 2.5 cm), along with stumps and logs bigger than 10 cm in base diameter, were labeled and mapped on x,y axes. For each individual, species, diameter at 50 cm height, dbh, total height, crown ratios and crown radii in four orthogonal directions were recorded. Decay classes for coarse woody debris ranging from 1 (most recent) to 5 (most decomposed) were estimated based on guidelines by Motta et al. (2006). Tree coordinates and measurements were stored in a spatial database (ArGIS 8.3).

Tree-scale analysis of competition was carried out on dendrochronological samples taken from two plots. An increment core was taken at 50 cm height from all living scots pine trees with dbh >7.5 cm trees. In the lab, following optimization of surface resolution, we measured radial increments to the nearest 0.01 mm. Data were collected and stored using a LINTAB device and the TSAP package (Rinn, 1996). The cores were cross-dated against available site chronologies (Tessier and Edouard, 2002) in order to ensure the assignment of the correct year to the each annual ring, both by visually checking the curves and by calculating the t-values relating to the coefficient of correlation (Baillie and Pilcher, 1973). 405 cores from the Morgex study area were successfully cross-dated; pines established in the S.Maria study area are much younger (98% of the cores have less than 50 growth rings), so reliable cross-dating was not possible (Fritts, 1976).

	Location	*UTM*	*Elevation [m]*	*Slope.*	*Aspect*	*Age*
1	Challand St. Anselme (AO)	5062482 N 402270 E	1116	40%	W	90
2	St.Denis (AO)	5068071 N 387870 E	985	62%	SW	30
3	St.Denis (AO)	5068444 N 389978 E	1350	34%	SW	125
4	Morgex (AO)	5069859 N 344753 E	1091	77%	S	90
5	Borgo Ticino (NO)	5060489 N 467254 E	320	flat	-	100
6	S. Maria Maggiore (VB)	5110657 N 457763 E	1050	40%	E	45
7	Toceno (VB)	5110964 N 458567 E	1050	80%	W	90-130
8	Trasquera (VB)	5118744 N 439503 E	1247	30%	SE	100-300

Table III.1 – Overview of permanent sample plots used in this study. Age of the stands was inferred from available documentation and forest management plans.

Stand-scale competition

Reconstruction of past stand development and current competition intensity was assessed both at the stand and at the individual tree level. At the stand scale, the overall intensity of competition was described by means of the relative SDI (Reineke, 1933; Shaw, 2006). We computed in each stand summation-based SDI (Shaw, 2006) for trees larger than 7.5 cm in dbh (both on Scots pine only and on all species combined). Relative density was represented by the ratio between such SDI and SDI_{max} for Scots pine (Vacchiano, 2007b).

The effect and response of competition were evaluated by assessing the structural and spatial features of the current stands. Size heterogeneity within a stand is considered the outcome of asymmetric competition, i.e., arising from light resource availability (Ford and Diggle, 1981; Weiner and Thomas, 1986; Yastrebov, 1996; Bauer et al., 2004). The inequality of dbh distributions (Scots pine only) was described by means of the Gini coefficient (Weiner and Solbrig, 1984):

$$[6] \qquad G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\left|d_i - d_j\right|}{2n(n-1)\cdot QMD}$$

where n is the number of trees measured,

d_i and d_j are the dbh of two subsequent tree records,

QMD is the quadratic mean diameter of the stand [cm].

G values are constrained between 0 (all individuals are equal) and 1 (maximum heterogeneity). To examine the location of size inequality among the dbh distributions, the cumulative dbh distributions were described as Lorenz curves (Weiner and Solbrig, 1984). In the Lorenz curve, individuals are ranked from the smallest to the largest. The cumulative fraction of the population is plotted against the cumulative fraction of the variable whose inequality is to be evaluated. If all individuals ware equal with respect to the specified variable, the curve would result in a diagonal line going from the origin to the upper right corner (Rouvinen and Kuuluvainen, 2005).

Several authors have shown that spatial structure, i.e., relative position of trees on the stand, results from past stand dynamics: establishment of young trees, competition for the different resources and death due to senescence or competition (Moeur, 1993; Pacala and Tilman, 1994; Batista and Maguire, 1998). We can thus assume that some of the characteristics of the stand spatial pattern reflect the major trends in its dynamics, and therefore wonder if some of these characteristics can be used as indicators of the dynamics. Regular spatial structures are commonly supposed to indicate high competition in stands, whereas aggregate patterns indicate massive regeneration without subsequent strong self-thinning (Leps and Kindlmann, 1987; Kenkel, 1988; Szwagrzyg and Czerwczak, 1993; Ward and Stephens, 1996; Pélissier, 1998). If competition is mainly for light and therefore one-sided or asymmetric (Weiner, 1990; Ford and Sorrensen, 1992; Schwinning and Fox, 1995), strong local regular patterns of surviving individuals develop from initially random or clumped patterns (Hutchings, 1979; Antonovics and Levin, 1980; He et al., 1997; Martens et al., 1997). There is general agreement that such pattern formation is driven by resource pre-emption and subsequent density-dependent mortality (Ford and Diggle, 1981; Watkinson et al., 1983; Hughes, 1988; Chapin et al., 1989; Kenkel et al., 1997; Little, 2002).

Spatial distribution patterns of *Pinus sylvestris* standing live and dead trees were characterized by means of used Ripley's K(t) function, based on the variance of tree-to-tree distances in a two-dimensional space (Ripley, 1977). The K value expresses the expected number of events in circular plots with radius *t* around each event. By calculating K for all radii the empirical K(t) function may be estimated (Ripley, 1981):

$$[7] \qquad K(t) = n^{-2} A \sum_{i \neq j} \sum I_t(u_{ij})$$

where n is the number of trees,

A the size of the study area (m^2),

u_{ij} the distance between plants i and j,

$I_t(u_{ij})$ an indicator variable which is 1 if $u_{ij} \leq t$ and 0 otherwise.

By comparing the K(t) function to an alternative spatial model it is possible to detect differences between the two. The null spatial model used in this study is the complete spatial randomness model (CSR), or Poisson process (Cressie, 1993; Wiegand and Moloney, 2004). In a random distribution, $K(t) = \pi t^2$.

In this study K(t) was replaced with L(t), a square root transformation that linearizes K(t) and stabilizes its variance (Legendre and Legendre, 1998). The empirical L(t) function is estimated for $t = 0 \ldots 20$ m, in steps of 1 m, and using a rectangular edge correction (Haase, 1995). A Monte Carlo simulation method was used to randomly generate CSR plots of the same dimensions as the observed one. We produced 200 Monte Carlo simulations to compare the value of the function L(t) with the one expected from a randomly distributed group of points. A plot of L(t) against t reveals spatial pattern at various values of the neighborhood distance t. Positive values of L(t) indicate regularity, while negative ones signify clumping (Kenkel, 1988). Statistical significance of the L(t) values was assessed in comparison with the 95% confidence envelopes for the random L(t) Monte Carlo-based simulation (Camarero et al., 2000).

To get information on the spatial relationships between different species we examined bivariate spatial interactions using $K_{12}(t)$, a generalization of K(t) for a bivariate point process (Diggle, 1983; Upton and Fingleton, 1985; Andersen, 1992). Values of $K_{12}(t)$ greater, equal or lower than the 95% confidence envelopes indicate respectively positive association (attraction), spatial independence or significant negative association (repulsion) between the two species analyzed (Duncan, 1991; Fortin et al., 2002). Combinations between *Pinus sylvestris* and the other species were analyzed in mixed stand; only significant spatial interactions are presented herein. All intertree distances were corrected for slope. Felled trees were not included in the analysis; broadleaved shoots sprouting from the same stump were considered as one individual. All analyses were performed using the software CrimeStat III (Levine, 2004).

To quantify the pattern of tree establishment, spatial autocorrelation between tree age was examined by means of Moran's I index (Cliff and Ord, 1981; Palmer, 1988; Legendre and Fortin, 1989). In this case, an intensity variable (age where applicable, dbh as a proxy otherwise) was attached to the coordinates of the tree (x, y); each individual was considered to represent its surrounding portion of space. Moran's I spatial autocorrelation coefficient ranges from -1 to +1, with zero being the expected value for no spatial autocorrelation (Upton and Fingleton, 1985; Camarero et al., 2000). A graph showing how autocorrelation changes as a function of distance, assuming spatial isotropy for the variable analyzed, was obtained for each plot; each autocorrelation coefficient of the correlogram was tested to show that its value is significantly different from zero. Moran correlograms for Scots pine trees were computed up to a 20 m distance (irregular lattice grid, lag = 1m) using the Rooks Case add-in package for Microsoft Excel (Sawada, 1998).

Last, the stand-average response of trees to competition was evaluated by plotting the relationship between individual relative growth rate (RGR) and size. RGR, defined as the increment per unit time per unit size, has long been recognized as a measure of growth efficiency that provides a sensitive measure of the response of trees to competition (Erickson, 1976; Ford, 1979; Harper, 1977; Cannell et al., 1984; Radosevich and Osteryoung, 1987). It is also believed that RGR adjusts for differences in initial size, environmental conditions or genetic inheritance (Ledig, 1974; Kramer and Kozlowski, 1979; Radosevich and Osteryoung, 1987). Since competition between plants in even-aged, pure stands is recognized to be fundamentally asymmetric (i.e., light is usually the most limiting resource) (Ford and Diggle, 1981; Weiner and Thomas, 1986; Connolly and Wayne, 1996; Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001), dominant plants should reduce smaller trees'

RGR more than vice versa. In free-growing plants, RGR should decrease with tree age and thus with increasing tree size (Zeide, 1993), since small trees are more efficient than large trees at producing new biomass before the onset of competition (as expressed by the sigmoidal individual growth curve). Conversely, when competition begins, the relationship of RGR with size should gradually invert its slope, since growth of smaller plants is more hampered by asymmetric competition (Schmitt et al., 1987). The effect of competition is therefore to reduce the efficiency of small trees relative to large trees (Larocque and Marshall, 1993). Even if some studies found that measures of growth efficiency in terms of *RGR* did not perform better than absolute growth rates (AGR) when used as response variable in growth models (Larocque, 2002), we examined the stand-level pattern of RGR in the two study plots were core samples had been taken and measured. We computed periodic RGR for the last 5, 10 and 30 years as follows:

$$RGR = \frac{\ln D_1 - \ln D_0}{years} \tag{8}$$

where RGR is percent relative growth rate of target tree,

D_1, D_0 [cm] are the diameter at 50 cm height at the end and at the beginning of the study period. The initial diameter was computed as $(D_1 - 2\Delta r)$, Δr being the radial increment over the selected time period [cm];

years is the length of the study period (5, 10, 30 years).

Tree-scale competition

In order to analyze competition dynamics at the individual tree scale and examine the impact of different neighbor-related predictors on focus tree performance, we used individual-based competition indices (CIs). The explicative power of a competition index is usually tested by how well it predicts the growth of subject tree (Huhn and Langner, 1999; Stadt et al., 2002). The set of indices (Table III.2) was selected from the literature in such a way to represent different combinations of tree variables (diameter, height, crown area, intertree distance) involved in influencing growth pattern. It is to be noted that the competition indices used do not explicitly separate above- form belowground resource competition (McPhee and Aarssen, 2001; but see Larocque, 2002).

We computed mean annual and periodic basal area increment (BAI) over the last 5, 10 and 30 years for all live Scots pine cored within a 50x50m subplot located at the center of each sample plot to avoid edge effects, i.e., unaccounted competitor neighborhood (Vanclay, 1991):

$$BAI = \pi \left[D\Delta r - (\Delta r)^2 \right] \tag{9}$$

where BAI is periodic basal area increment [cm^2],

D is tree diameter at 50cm height [cm],

Δr is radial increment over the selected time period [cm].

BAI distribution was normalized by logarithmic transformation; the logarithm of the basal area increment is considered one of the best variables reflecting the nonlinear curve of tree growth (Cole and Stage, 1972; Wykoff, 1990) and has got desirable properties with the error structure, e.g., homogeneous variance (Monserud and Sterba, 1996).

Index	Source	Variables	Equation
Daniels	Daniels et al. (1986)	Dbh	$\frac{D_i^2 \cdot n}{\sum_{j=1}^{n} D_j^2}$
Hegyi	Hegyi (1974)	Distance, dbh	$\sum_{j=1}^{n} \frac{D_j / D_i}{(L_{ij}+1)}$
R.K.$_1$	Rouvinen and Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^{n} \frac{D_j / D_i}{L_{ij}^2}$
R.K.$_2$	Rouvinen and Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^{n} \frac{(D_j / D_i)^2}{L_{ij}}$
P.K.	Pukkala and Kolström (1987)	Distance, height	$\sum_{j=1}^{n} \arctan \frac{(H_j - H_i)}{L_{ij}}$
CCS	Alvarez et al. (2003)	Distance, crown area[6]	$\sum_{j=1}^{n} \frac{A_j}{A_i \cdot L_{ij}}$
CAI	Castagneri et al. (2007)	Distance, crown area, height	$\sum_{j=1}^{n} \frac{\left(\frac{A_j \cdot H_j}{A_i \cdot H_i}\right)^2}{L_{ij}}$

Table III.2 – Competition indices used, tree variables involved and corresponding formulation. Key to symbols: n*, number of competitors;* D_i*, subject tree dbh [cm];* D_j*, competitor tree dbh [cm];* L_{ij}*, distance between competitor and subject tree [m];* H_i*, subject tree height [m],* H_j*, competitor tree height [m];* A_i*, subject tree crown area [m²];* A_j*, competitor tree crown area [m²].*

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[6] Crown projection area was computed as for an ellipse: $A = \pi \frac{r_1 + r_3}{2} \frac{r_2 + r_4}{2}$, where $r_1 \ldots r_4$ are crown radii in the four cardinal directions.

A large variety of mathematical models have been used to describe individual tree increment (Vanclay, 1994; Zhang et al., 2004), but the models may be reduced to entail only two opposing factors: the biological potential for unlimited multiplicative growth and a reduction due to competitive and environmental constraints (Zeide, 1993). This growth pattern is best modeled by a function with a multiplicative term and an exponential dampening, with the resulting growth curve having a sigmoidal form but no asymptote. Diameter or basal area increment was modeled as an exponential function of tree size, competition and site factors by a number of studies (Wykoff, 1990; Stoll et al., 1994; Vanclay, 1994; Monserud and Sterba, 1996; Jogiste, 2000; Andreassen and Tomter, 2003; Mailly et al., 2003; Zhang et al., 2004; Canham et al., 2006).

The explicative power of each CI was tested through a log-linear basal area increment model, whose predictor variables were representative of focus tree's size and perceived competition:

$$[10] \qquad \ln BAI_{periodic} = a_0 + a_1 \ln dbh + bCI$$

where dbh is focus tree's diameter at breast height [cm],

CI is the value of the competition measure being used for the *i*-th focus tree,

a_0, a_1, b are regression coefficients.

The presence of a size predictor is related to the positive size-dependency of growth rates in plants (Harper, 1977), i.e., growth of an individual is directly related to its size, which is an expression of light capture and foraging ability or success (Pfister and Stevens, 2002). Inclusion of a size variable accounts for the growth potential of an ideally open-grown tree; the incorporation of focus tree size in most competition indices is also able to account for the age-related decline of tree growth (Nord-Larsen, 2006). The obvious drawback is that the ageing and competition effects on growth are difficult to tell apart, because expressed by a common measure. Models using only a CI as growth predictor are even more difficult to interpret, because one index simultaneously expresses the effects of size-dependency, ageing and competition.

Since not all competitor tree variables used in CI computation could be backdated, all the predictors reflect tree measurement at the end of the analysis period. The model was fit with an ordinary least-squares method using a stepwise approach; the fit was computed for the two sites under analysis separately, therefore predictors related to site morphology or fertility class were omitted from the model because they were deemed as constant.

The importance of competition acting in the stands (*sensu* Welden et al., 1988) was evaluated from the improvement in overall goodness-of-fit (adjusted R^2) generated by each of the competition measures entering the stepwise model. Significance of regression coefficients was evaluated to the 95% confidence level; the standardized coefficients associated to the most informative competition measures were compared across sites to assess the absolute intensity of competition on focus Scots pines.

When computing competition indices, only trees growing inside the “zone of perception” (Hara, 1988; Burton, 1993) of the focus tree were selected as competitors. Among the different methods proposed for competitor selection (for a complete review see Biging, Dobbertin, 1992; Alvarez et al., 2003; Corral Rivas et al., 2005), we adopted two fixed and one variable search radii for identify such zone. Fixed radii were set to 5 and 10 m according to available literature (Pukkala and Kolstrom, 1987; Stoll et al., 1994; Rouvinen and Kuuluvainen, 1997; Prévosto et al., 2000). We also recurred to the influence-zone concept proposed by Stæbler (1951), i.e., the bidimensional surface within which trees compete for environmental resources (Ottorini, 1978). Competition is assumed to exist when the zones of influence of two trees overlap, i.e., when the sum of the influence radii of two neighbor trees is lower than the distance between them. Many authors defined the zone of influence as a circular area surrounding the tree with a radius equal to the crown radius of an open-grown tree of the same diameter (Holmes and Reed, 1991; Larocque, 2002; Corral Rivas et al., 2005) or the same height (Ek and Monserud, 1974), i.e., the potential rather than actual competitive radius of the tree (Antonovics and Levin, 1980). In order to calculate the size of open-grown crowns and their overlap, we used the allometric equations proposed by Hasenauer (1997) for Scots pine and other species[7] in the Austrian Alps, an area both geographically and climatologically similar to the one studied herein:

$$[11] \qquad OCA = \pi\left(e^{-0.0201+0.7317\ln H}\right)^2$$

where OCA is crown area of an open-grown Scots pine [m^2],

H is total tree height [m].

The referenced model for Scots pine has a RMSE of 1.04 m (Hasenauer, 1997). We chose tree height, rather than dbh, as the predictor variable because it is less influenced by the degree of crowding experienced during tree development (Assmann, 1970), and therefore it is a better expression of a tree’s maximum crown size. The trees whose zone of influence intersected the open-grown crown of focal tree were chosen as competitors.

Trees in the 10m-wide buffer zone surrounding the subplot were used in calculating competition indices, but not as focus trees in the modeling of crown dimensions. The three described criteria were applied to all the CIs used, in order to evaluate the most effective selection method in computing competitive

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[7] Species not modeled by Hasenauer’s equations were mapped to similar shaped species (e.g., Wild Cherry [*Prunus avium* L.] to Sycamore Maple [*Acer pseudoplatanus* L.]).

influence and to have ecological insights on the size of the influence zone for this species. Trees with missing measurements (dbh, height or crown data) were excluded from both the focus trees and the competitors samples; where applicable, competition intensity acting on recently dead trees (standing snags) was evaluated by plotting the distribution of the CI for focus snags and comparing it with the CI distribution for live trees in the plot.

In both plots, a full 30-years BAI model was developed using the best available combination of competition index and selection method, adding tree size, age, live crown ratio, and a stand density-related predictor (percentile rank of focus tree's diameter on overall stand dbh distribution), which were used by many authors as effective BAI predictors (Wykoff et al., 1990; Hann and Larsen, 1991; Corral Rivas et al., 2005):

$$\begin{aligned} \ln BAI_{30} &= a_0 + a_1 \ln D_{50} + a_2 CI + a_3 age_{50} + \\ &+ a_4 LCR + a_5 rank_{\%} \end{aligned} \tag{12}$$

where BAI_{30} is individual basal area increment in the last 30 years [cm^2],

D_{50} is tree diameter at 50 cm height [cm],

CI is the competition index used,

age_{50} is tree age at 50 cm height,

LCR is live crown ratio (computed from the height of the lowest living branch in whatever direction as measured in the field),

$Rank_{\%}$ is the percentile represented by the tree's diameter in the stand diameter distribution.

All predictor variables were measured at the end of the growth period, representing the tree's current status rather than its initial conditions. The model was fit through stepwise OLS regression for the two study areas separately. To evaluate the performance of the fits the root mean square error (RMSE) [13] and the adjusted coefficient of determination (R^2_{adj}) were estimated and compared with the same indices obtained from two null models, including respectively tree size only, and tree size and the selected competition index.

$$RMSE = \sqrt{\sum \frac{\left(y_i - \hat{y}_i\right)^2}{n-p}} \qquad [13]$$

where y_i and y_i^ are the measured and predicted values of the dependent variable, respectively,

n is the total number of observations used to fit the model,

p is the number of model parameters.

The variance inflation factors (VIF) of all the independent variables were calculated for detecting multicollinearity [14]; values up to 10 were accepted (Draper and Smith, 1998; Belsey, 1991; Soares and Tomé, 2001).

$$VIF = \frac{1}{1-R_i^2} \qquad [14]$$

where R^2_i is the multiple correlation coefficient obtained when the *i*-th independent variable X_i is regressed against all the remaining independent variables in the individual tree growth model.

Results

We labeled, mapped and measured more than 7,300 elements in the permanent plots. Tables III.3 and III.4 summarize data on live and dead trees respectively; a detailed description of each plot is given at the following pages, along with graphs for species composition based on basal area (left) and tree number (right), and live and dead tree size distributions. Coarse woody debris was apportioned by size class; we highlighted size distribution of cut stumps, recently dead trees (i.e., logs and snags in the first decay class) and the ratio of natural deaths to the number of living trees for each size class. Finally, a tridimensional reconstruction of the stands was carried out by using the software Stand Visualization System 3.36 (McGaughey, 2002).

Plot	**Density**		**Basal area**		**QMD**		**Relative density**		**H_{top}**	**Cover**
	[trees ha^{-1}]		[m^2 ha^{-1}]		[cm]				[m]	
Challand	724	*573*	42.3	*35.3*	27.3	*28.0*	.56	*.47*	17.6	82%
St.Denis I	1400	*876*	18.0	*13.6*	12.8	*14.0*	.34	*.25*	7.8	66%
St.Denis II	933	*929*	35.7	*35.7*	22.1	*22.1*	.53	*.53*	14.2	55%
Morgex	824	*610*	36.8	*34.1*	23.8	*26.7*	.53	*.48*	16.7	81%
B.Ticino	716	*357*	33.8	*27.3*	24.5	*31.2*	.47	*.39*	24.6	97%
S.Maria	861	*827*	38.5	*37.6*	23.9	*24.1*	.56	*.55*	17.9	93%
Toceno	765	*720*	70.6	*69.8*	34.3	*35.1*	.90	*.89*	22.7	78%
Trasquera	343	*306*	33.3	*32.9*	35.2	*37.0*	.40	*.39*	24.2	77%

Table III.3 – Summary data for living trees in the permanent plots under study (trees larger than 7.5 cm in dbh); data for all trees and Scots pine only (in italics). Relative density is represented by the ratio of observed to maximum Stand Density Index (SDI), calculated by the summation method (Vacchiano, 2007b). Crown cover is the plot-wise figure computed by summing individual crown projections.

Plot	**CWD Basal area** [m^2 ha^{-1}]	**Snags**	**Cut stumps**	**Yearly mortality**
Challand	24.16	39	6	5%
St.Denis (lower)	7.10	122	6	15%
St.Denis (upper)	16.88	71	259	n.d.
Morgex	7.12	80	67	1%
Borgo Ticino	1.40	31	8	1%
S.Maria	10.10	61	92	26%
Toceno	12.47	20	161	2%
Trasquera	10.71	0	104	n.d.

Table III.4 – Summary data for coarse woody debris (Scots pine only) in the permanent plots under study (stumps and logs larger than 10 cm in dbh, all decay classes). Snags only account for natural mortality. Yearly mortality rates based on repeated inventories (re-entry time 3 to 12 months). All data are computed on a per-hectare basis.

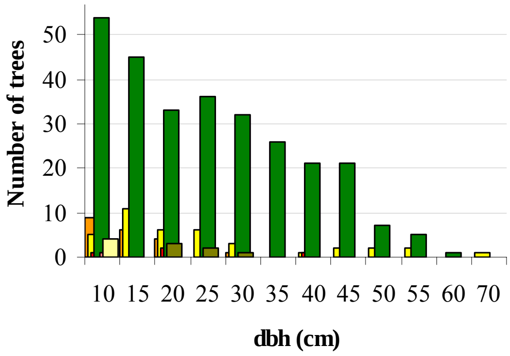
Dbh distribution analysis showed that in most plots Scots pine is characterized by an unimodal, symmetric size distribution. In Challand and St.Denis I the distribution is heavily skewed to the right, up to the point of behaving more like a J-shaped, uneven-aged-like size distribution. Plots where pine regeneration gathers in dense patches (St. Denis II, Trasquera) show a bimodal distribution. Broadleaves, which are usually subordinated, are a dynamic part of the stand in all cases; establishment pattern is gradual but steady and shows a J-shaped pattern, which is more pronounced where succession is more advanced.

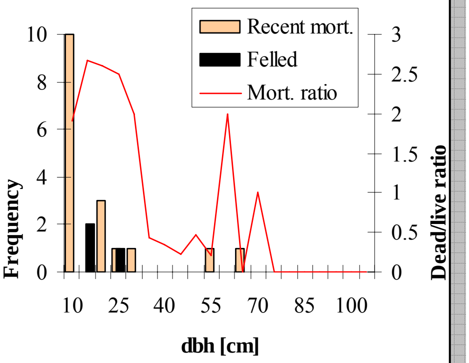
The intensity of anthropogenic disturbance to the stands (evidence brought by cut stumps) varies from negligible (e.g., St.Denis I) to very high (e.g., Trasquera). Natural mortality shows two major trends: either smaller trees are more prone to die, or the pattern of recently dead trees follows the shape of living tree size distribution (e.g., Borgo Ticino).

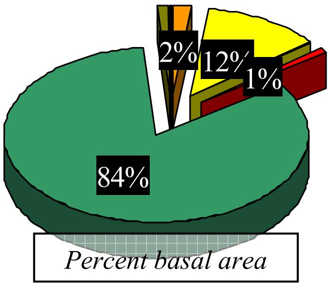
Challand St. Anselme

Forest type cover: Middle-alpine Scots pine on acid soils (*Dechampsio-pinion*)

The stand is located on a west-facing slope; a cliff directly above the stand is a source of frequent rockfall events and determines the formation of scree slopes. These give a gappy appearance to the stand's horizontal structure; gaps are sometimes filled by Aspen (*Populus tremula* L.). Yearly rainfall is usually higher than 800 mm; the acid soil favors chestnut (*Castanea sativa* Miller) on lower elevations, where small orchards were once grown. The stand has been heavily grazed in the past.







Percent basal area

🟧 casa
🟨 lade
🟥 piab
🟩 pisy
🟫 potr
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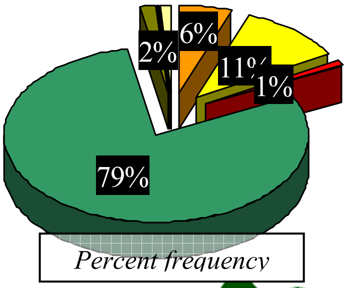
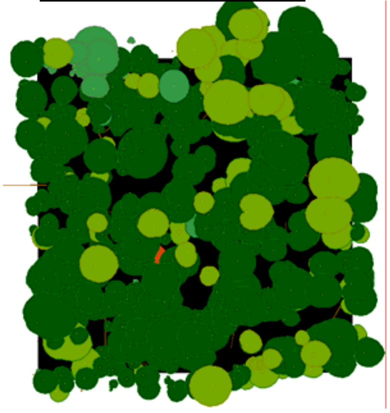
⬜ soar



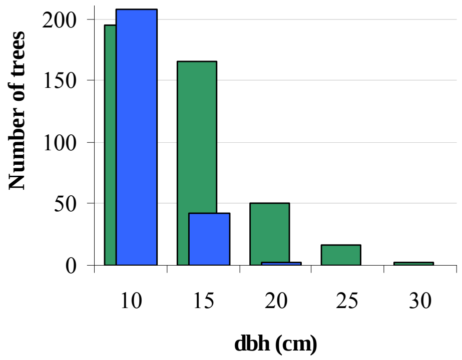
Percent frequency

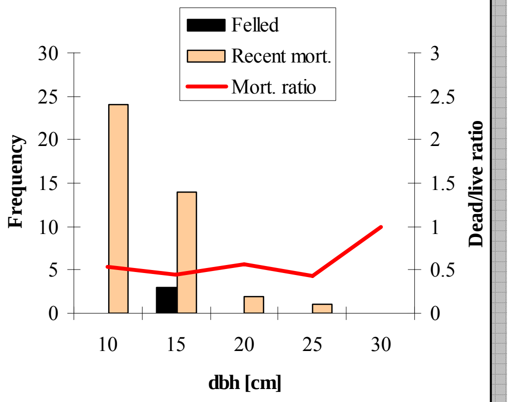


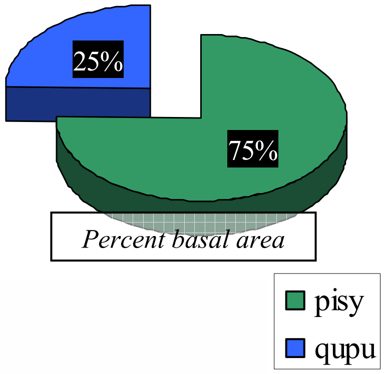
St.Denis I

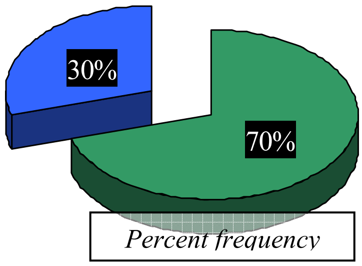
Forest type cover: Inner-alpine Scots pine on alkaline soils (*Ononido-pinion*)

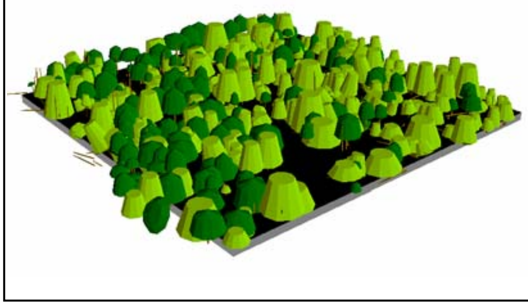
Young stand originated by secondary invasion by pine and Downy Oak (*Quercus pubescens* Willd.) not earlier than 30 years ago and never managed thenceforth. The site is located in the aridest area of the region (400 mm year^{-1}); high density and extremely low soil fertility result in poor health conditions for most individuals. Tree pattern is locally dense, but large gaps are present where the soil is too shallow to allow tree colonization.







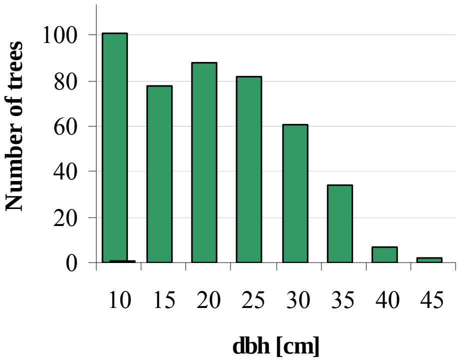


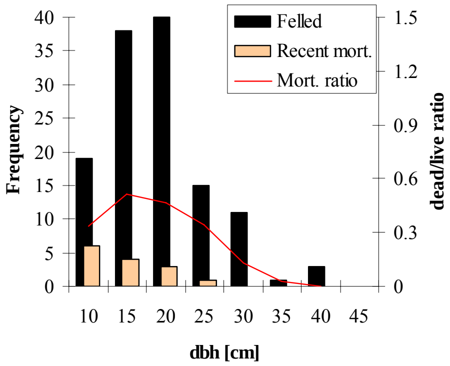


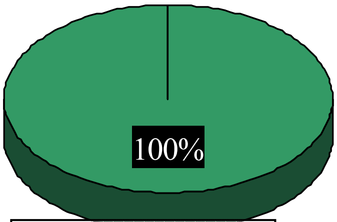
St.Denis II

Forest type cover: Inner-alpine Scots pine on alkaline soils, variant with spruce

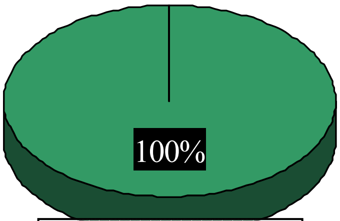
Mature Scots pine stand, patterned in many even-aged patches. Large groups of mature trees alternate with dense regeneration thickets, the latter establishing where light levels on the ground are higher. Tree growth is slow because of site-related drought; disturbances often disrupt stand structure, either by wind- or snow-induced uprooting, or by frequent crown fires.



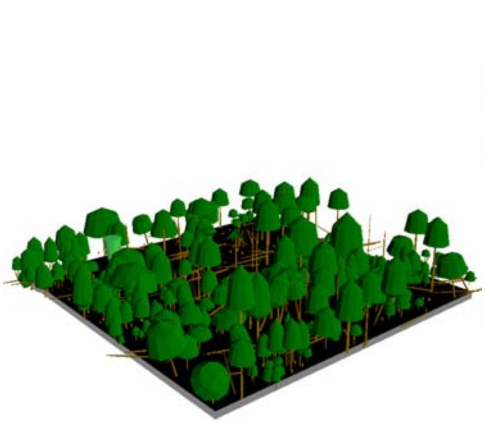


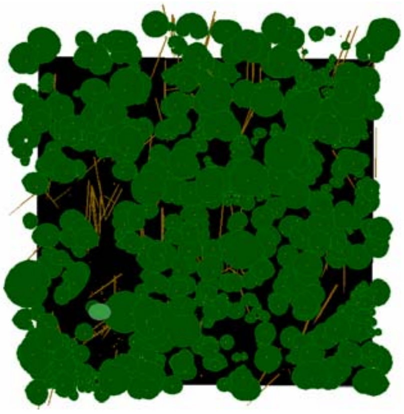


Percent basal area



Percent frequency

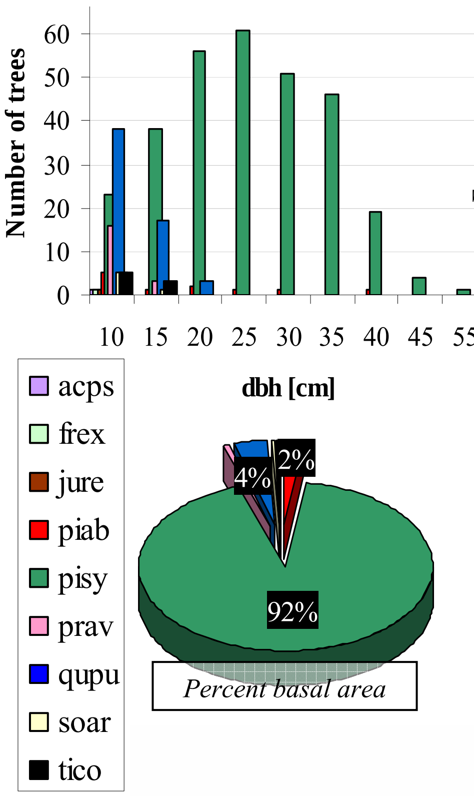


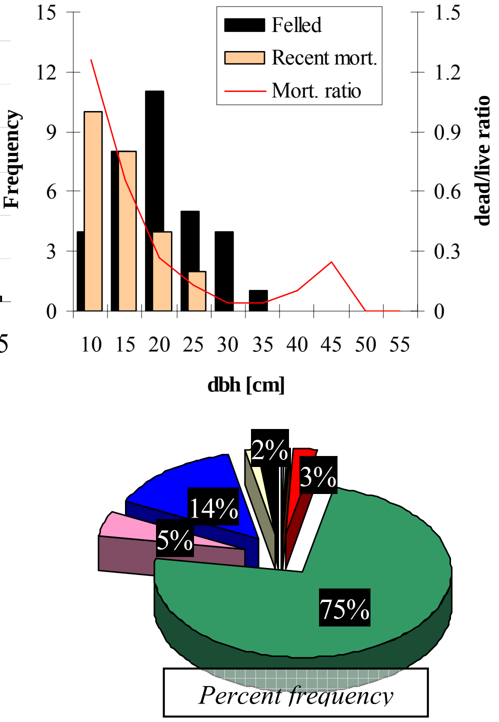


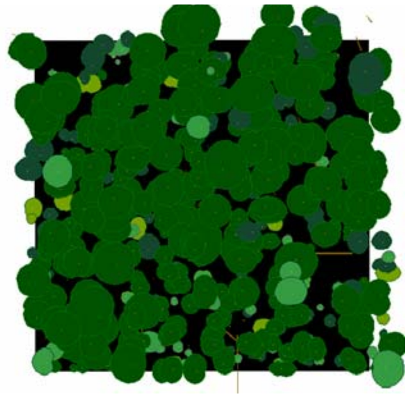
Morgex

Forest type cover: Inner-alpine Scots pine on alkaline soils

The upper canopy layer is dominated by Scots pine, but downy oak and other late-seral broadleaves (Sycamore Maple [*Acer pseudoplatanus* L.], Wild Cherry [*Prunus aviums* L.], rowans [*Sorbus* spp.], Little-leaf Linden [*Tilia cordata* Miller], English Walnut [*Juglans regia* L.]) have been establishing in the understory for the last decades and have n reached codominant status. The stand is bordered by an active avalanche channel Intense logging for charcoal purposes, grazing and litter collection have been replaced in recent years by frequent but limited group selection cutting (Saponeri, 2006).



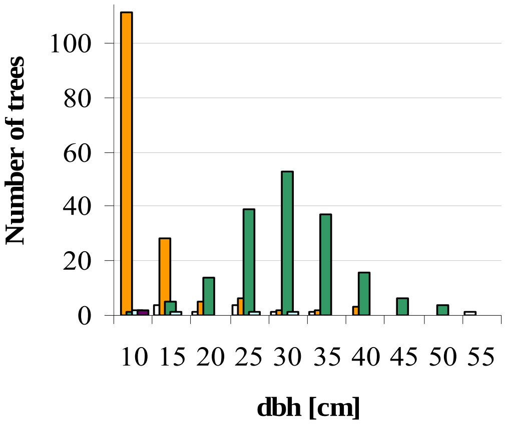


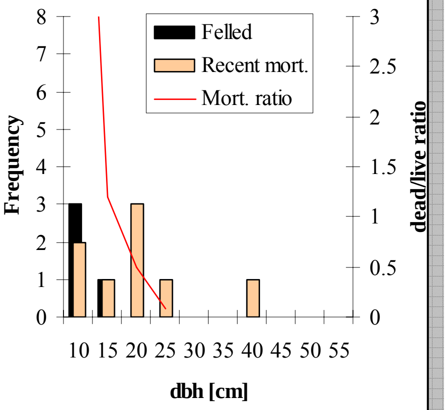


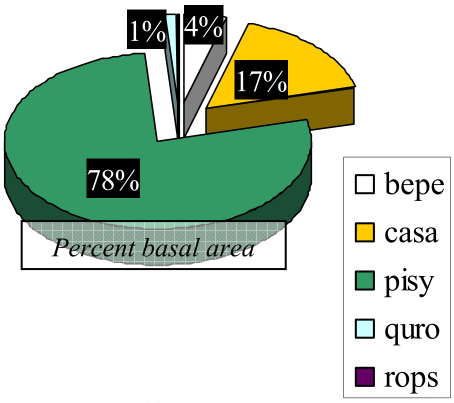
Borgo Ticino

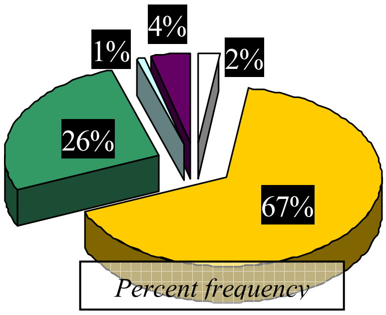
Forest type cover: Scots pine on moorland

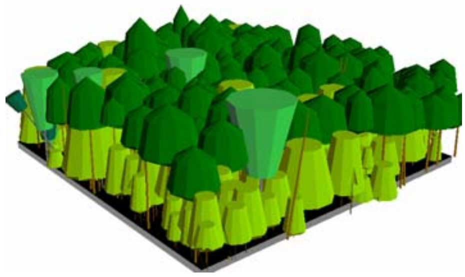
The upper layer is represented by a mature even-aged Scots pine; the understory and regeneration layers are occupied uniquely by Chestnut and sparse Pedunculate Oak (*Quercus robur* L.). Frequent low fires thinned the pines and favored the establishment of broadleaves, which were further extended by intense coppicing. Residual pines are characterized by high crowns, thick bark and poor self-pruning due to negative selection. Succession to a broadleaved stand is foreseeable.

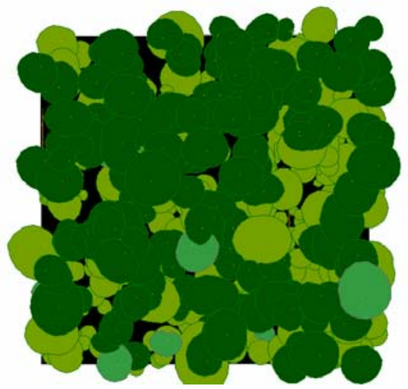








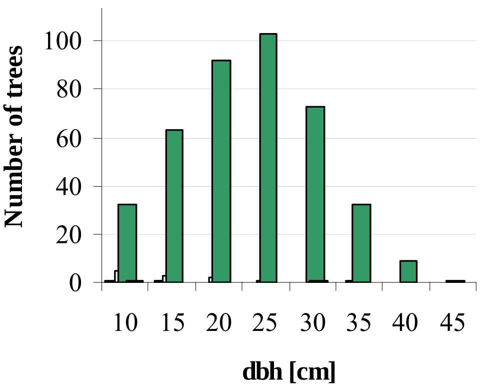


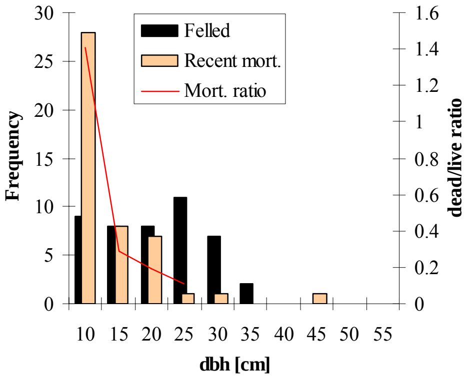


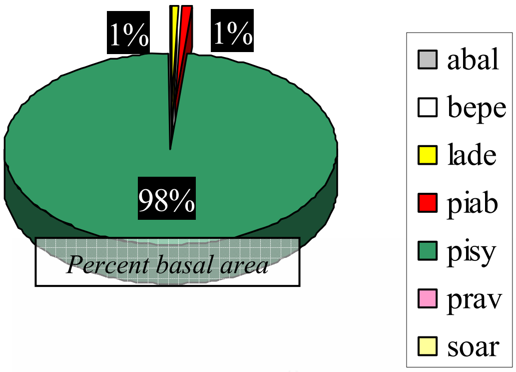
S. Maria Maggiore

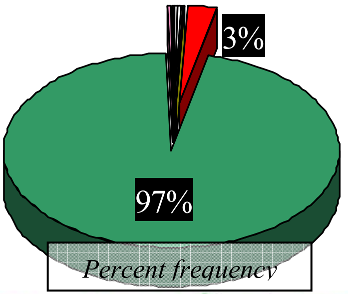
Forest type cover: Middle-alpine Scots pine on acid soils

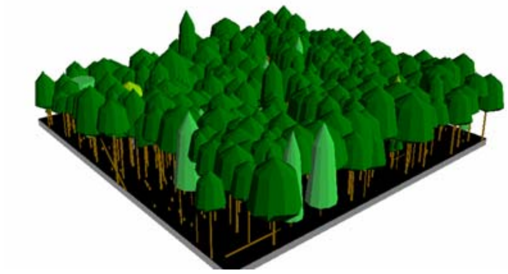
Dense, young Scots pine stand established on a previously non-forested slope. Mature stands in the higher part of this valley were the seed source for seedling establishment, which started about 50 years ago after the abandonment of farming and grazing practices. High rainfall amounts (1800 mm year^{-1}) allow quick and steady growth; low light levels under the dense, monolayered canopies are suitable for regeneration of late-seral conifers (Silver Fir [*Abies alba* Miller] and Norway Spruce). Sporadic cutting has been carried on to stimulate regeneration of late-seral species and as a measure to contrast Pine processionary moth (*Traumatocampa pityocampa* Den. & Schiff.) outbreaks.

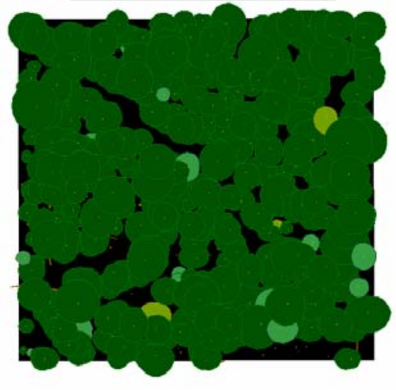








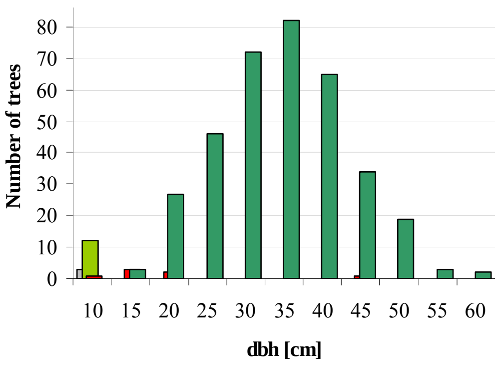


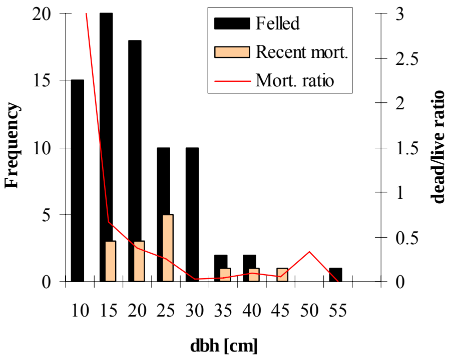


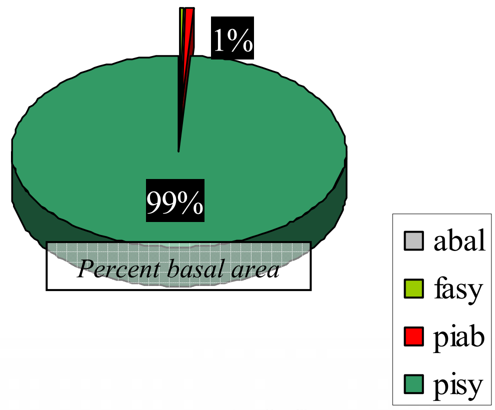
Toceno

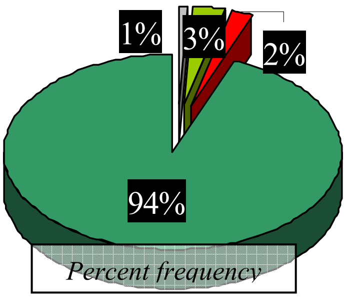
Forest type cover: Middle-alpine Scots pine on acid soils

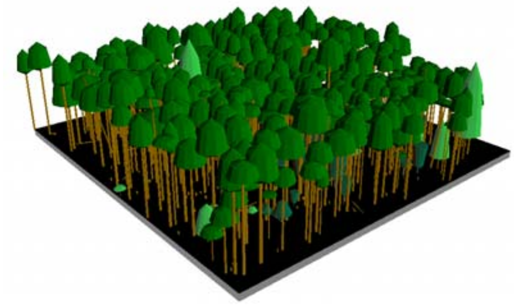
Mature Scot pine stand on a steep slope; high fertility (see previous area) stimulate rapid height growth and optima stem form. Man could have favored pine for the practice of tapping (resin production lasted until World War II; scars suggest the stand is 90 to 120 years old). Spruce is present in small groups; Silver Fir and European Beech (*Fagus sylvatica* L.) seedlings are scattered throughout the stand. Diffuse evidence of single-tree selection cutting.

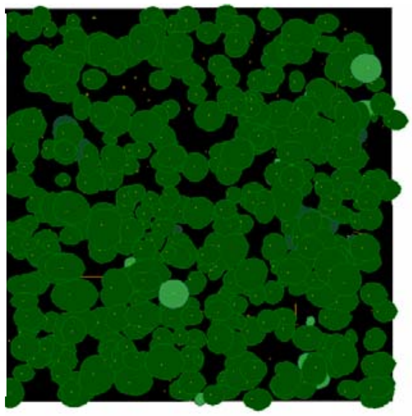








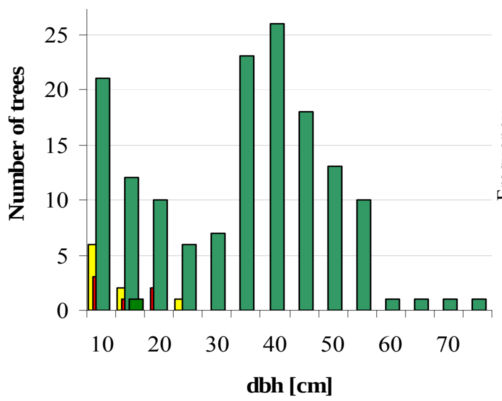


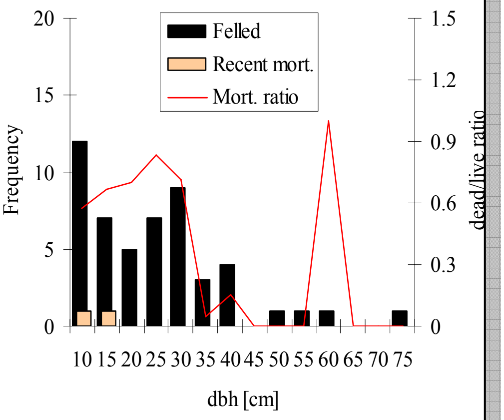


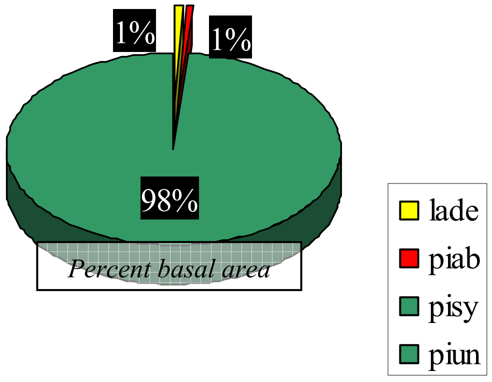
Trasquera

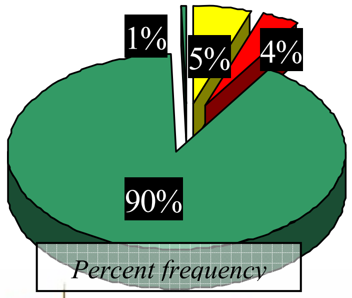
Forest type cover: Middle-alpine Scots pine on acid soils

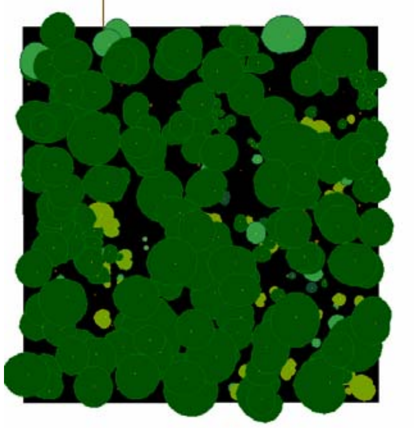
The structure is markedly two-storied, with a sparse mature overstory and dense regeneration patches establishing in the gaps. European larch (*Larix decidua* Miller) and Norway Spruce saplings may be found on mineral soil, but are often suppressed by the wide crowns of the overtopping pines. Tree cores from mature Scots pines in the stand (Motta et al., 1999) were found to be up to 300 years old. The stand was disturbed in the last 20 years by repeated selective loggings.











Gini coefficient [Table III.5] ranges from 0.21 to 0.48. Size distributions of pine trees show different degrees of inequality, which is sometimes strongly emphasized (but never attenuated) when the broadleaved component is included. Higher GCs expectedly reflect two-storied stand structures. Figure 23 shows Lorenz curves for the study areas as compared with a perfectly uniform size distribution; a similarity between monolayered stands and a greater relative contribution of seedlings in two-layered or patchy stands are evident features.

Plot	**GC All trees**	**GC Scots pine**	**GC Other species**
Challand	0.39	0.37	0.34 (*Larix d.*)
St.Denis (lower)	0.29	0.25	0.25 (*Quercus pub.*)
St.Denis (upper)	0.43	0.43	-
Morgex	0.38	0.29	0.25 (*Quercus pub.*)
Borgo Ticino	0.47	0.13	0.34 (*Castanea s.*)
S.Maria	0.22	0.20	-
Toceno	0.21	0.14	-
Trasquera	0.48	0.44	0.34 (*Larix d.*)

Table III.5 – Gini Coefficient of inequality (GC) in the study areas for all trees (dbh >2.5 cm), Scots pine only and selected accompanying species.

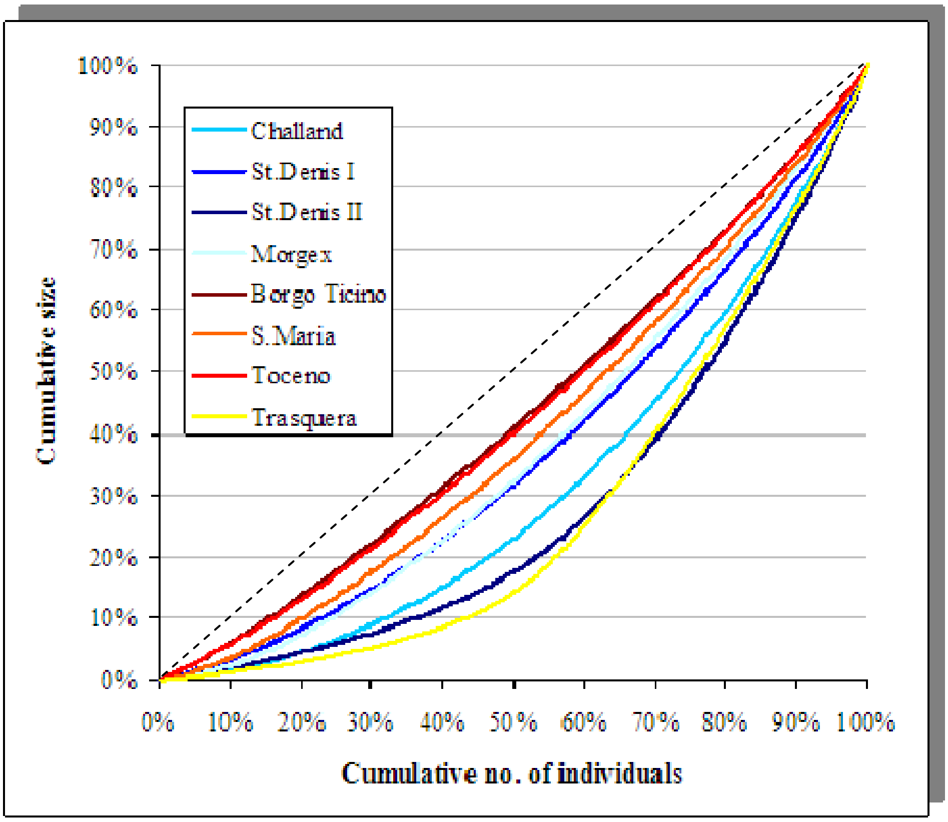


Figure 23 – Lorenz curves for size inequality in the study areas (trees larger than 2.5cm in dbh). Dashed line represents zero inequality (uniform dbh distribution); the area enclosed between this line and each Lorenz curve is equal to GC.

Spatial pattern of living Scots pine trees [Table III.6] was in most cases clumped on all spatial scales. S.Maria and Toceno showed a different trend (regular pattern over short distances), while no significant pattern was detected for Borgo Ticino and Morgex, apart from clumping at very large and very short distances respectively.

UNIVARIATE PATTERN (live Scots pine)

Site	*t [m]*																			
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*
Challand	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
St.Denis I	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
St.Denis II	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Morgex	+	+	+																	
Borgo Ticino																		+	+	+
S.Maria	●	●	●																	
Toceno	●	●	●	●																
Trasquera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

UNIVARIATE PATTERN (Scots pine snags)

Site	*t [m]*																			
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*
Challand																				
St.Denis I	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
St.Denis II		+	+	+	+	+	+		+											
Morgex	+		+		+	+	+	+	+			+	+	+	+	+	+	+	+	+
S.Maria	+	+	+	+	+	+	+	+	+	+	+	+								

BIVARIATE PATTERN

Site	*Interaction*	*t [m]*											
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Challand	PS-Broadleaved		−	−	−	−	−		−	−	−	−	−
St.Denis I	PS-Downy oak	+	+			+	+	+	+	+	+	+	
Morgex	PS-Downy oak												
Borgo Ticino	PS-Chestnut	−	−	−	−	−	−	−	−	−	−	−	−
Toceno	PS-Late seral											+	+

Table III.6: Univariate and bivariate Ripley's L(t) analysis for spatial point pattern of living and dead standing Scots pine tree (dbh >2.5 cm). +: clumping (univariate)/aggregation (bivariate), ●: overdispersion (univariate); −: repulsion (bivariate). Non significant values of L(t) and $L_{12}(t)$ are not shown in the table (p <0.95). Spatial point pattern analysis (SPPA) was run on standing *snags (univariate) and on other tree species (bivariate) only where these were present in sufficient number.*

Pine mortality (univariate SPPA on snags) followed a clustered pattern in four plots out of five analyzed (the others did not present a sample large enough). Mortality was found to happen in clumps up to mid distances in St.Denis II and S.Maria, and for all distances in St.Denis I and Morgex. Overdispersed mortality did not occur in the analyzed plots.

As for spatial relationship between different species, a significant spatial segregation was found between Scots pine and the broadleaved component in Challand and Borgo Ticino (repulsion from 1 to 12 m). Downy oak, on the opposite, exhibits an attraction pattern with Scots pine at least in one plot.

Dendrochronological analyses were carried out on a total of 358 samples, 167 of which where correctly cross-dated (see Methods). All size and age classes were represented in the sample [Table III.7]; trees in S.Maria area are much younger than individuals in Morgex and in the last 30 years experienced basal area increments twice as sustained as in the latter plot. Mean annual BAI spans over two magnitudes, ranging from 0.45 to 45.3 cm^2 $year^{-1}$. Though lower in average magnitude, increments in Morgex were much more variable than in S.Maria, both between individual trees (coefficient of variation of periodic BAI) and from year to year (mean CV of annual radial increments over the whole lifespan of selected tree). Regarding competitor selection, a 10m fixed radius typically selects the most individuals (but with greater variability in competitors number), a 5m radius the least and the potential crown area intersection rule an intermediate number between the two.

Morgex (n =167)	**Mean**	**SD**	**CV**	**Min**	**Max**
D_{50} [cm]	28.1	9.1	32.4%	9.5	49.5
Age_{50} [years]	80	29	36.3%	33	185
CV radial increment	61.8%	19.9%		25.2%	147.4%
BAI_5 [cm^2]	27.24	21.83	80.1%	2.25	125.25
BAI_{10} [cm^2]	59.19	45.31	76.6%	5.22	226.27
BAI_{30} [cm^2]	185.53	124.32	67.0%	16.80	606.73
# competitors (5m)	6.7	2.6		1	14
# competitors (10m)	28.1	4.8		15	40
# competitors (OCA)	9.4	3.2	3.2	2	17

S.Maria (n =191)	**Mean**	**SD**	**CV**	**Min**	**Max**
D_{50} [cm]	26.9	7.6	28.3%	10.5	45.0
Age_{50} [years]	36	4	11.1%	20	48
CV radial increment	43.2%	15.4%		15.2%	108.3%
BAI_5 [cm^2]	59.12	40.22	68.0%	3.33	174.45
BAI_{10} [cm^2]	140.86	86.55	61.4%	6.61	406.61
BAI_{30} [cm^2] [8]	470.40	250.54	53.3%	39.00	1356.79
# competitors (5m)	6.3	2.3		2	12
# competitors (10m)	25.8	5.0		13	39
# competitors (OCA)	12.2	4.0		3	21

Table III.7 – Summary characteristics of the sample used for individual-scale competition analysis (Scots pine only). D_{50}: diameter at 50 cm height; Age_{50}: age count at 50 cm height; CV: coefficient of variation for annual radial increment of single trees as measured by core analysis; BAI_{xx}: periodic basal area increment; # competitors: number of competitors selected by different distance criteria.

Dendrochronological analysis allowed the reconstruction of stand establishment, based on age at 50 cm height. The age of trees smaller than 7.5 cm in dbh, which were not cored, was computed by a power model relating Age_{50} and dbh [Figure 24]. The establishment of current stand in Morgex

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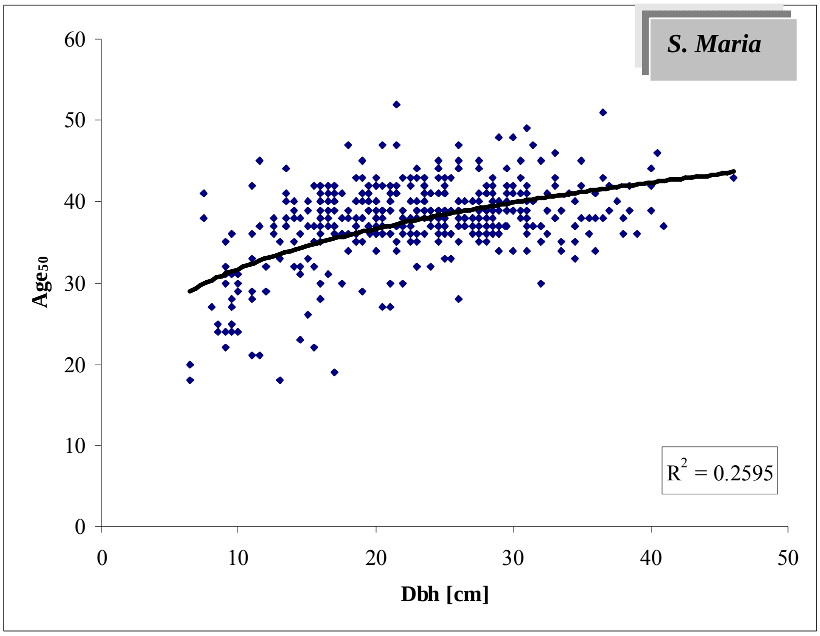
[8] BAI_{30} was calculated only for trees reaching 30 years of age (n =176).

started around year 1820, peaked in 1915-25 and slowly decreased until present days. Downy oak and other broadleaves are increasing their participation in the lower layers. On the other hand, the stand in S.Maria established over a fairly short amount of time and is therefore strictly even-aged; few individuals of other early-seral species have taken part in initial afforestation (i.e., Birch [*Betula pendula* Roth.]) or established on favorable seedbed at the beginning of stand establishment (like Norway Spruce and Larch) [Figure 25].

The temporal pattern of tree establishment was also reconstructed by means of Moran's correlograms, portraying spatial autocorrelation between tree age (or dbh) at different distances. Where both variables have been used, the correlograms did not show significant differences between age and dbh spatial trends, dbh showing attenuated pattern probably because of the "masking" effect of competition on diameter growth [Figure 26]. Therefore, the analysis was extended to all the others study areas using dbh as a proxy intensity variable where dendrochronological analyses had not been carried out. Significant positive autocorrelation was found to occur in a wave pattern (Legendre and Fortin, 1989) in S.Maria and Toceno, while the shape of correlogram is more similar to a gradient type in St.Denis II and Trasquera. A single spike on very short distances was found in Challand; no significant pattern was detected in the remaining plots. Negative autocorrelation has not been found but in isolated spikes on distances of about 12 to 18 m.



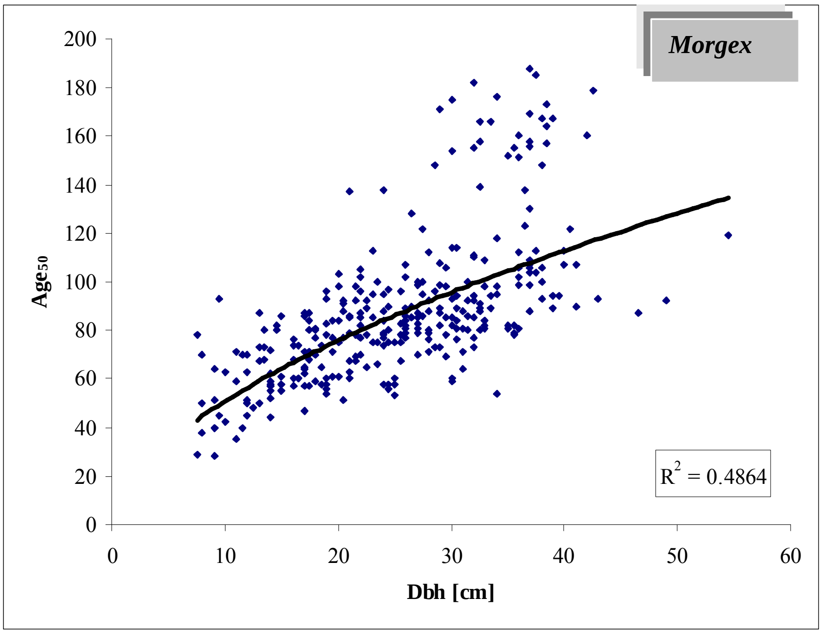


Figure 24 – Relationship between dbh and age at 50 cm height in the study areas (power model: $\mathrm{Age}_{50} = \mathrm{a\ DBH}^{b}$*). Goodness of fit is higher in Morgex. The analysis was carried out on all Scots pine cores sampled (n =319 and n =456 in the first and second plot respectively).*

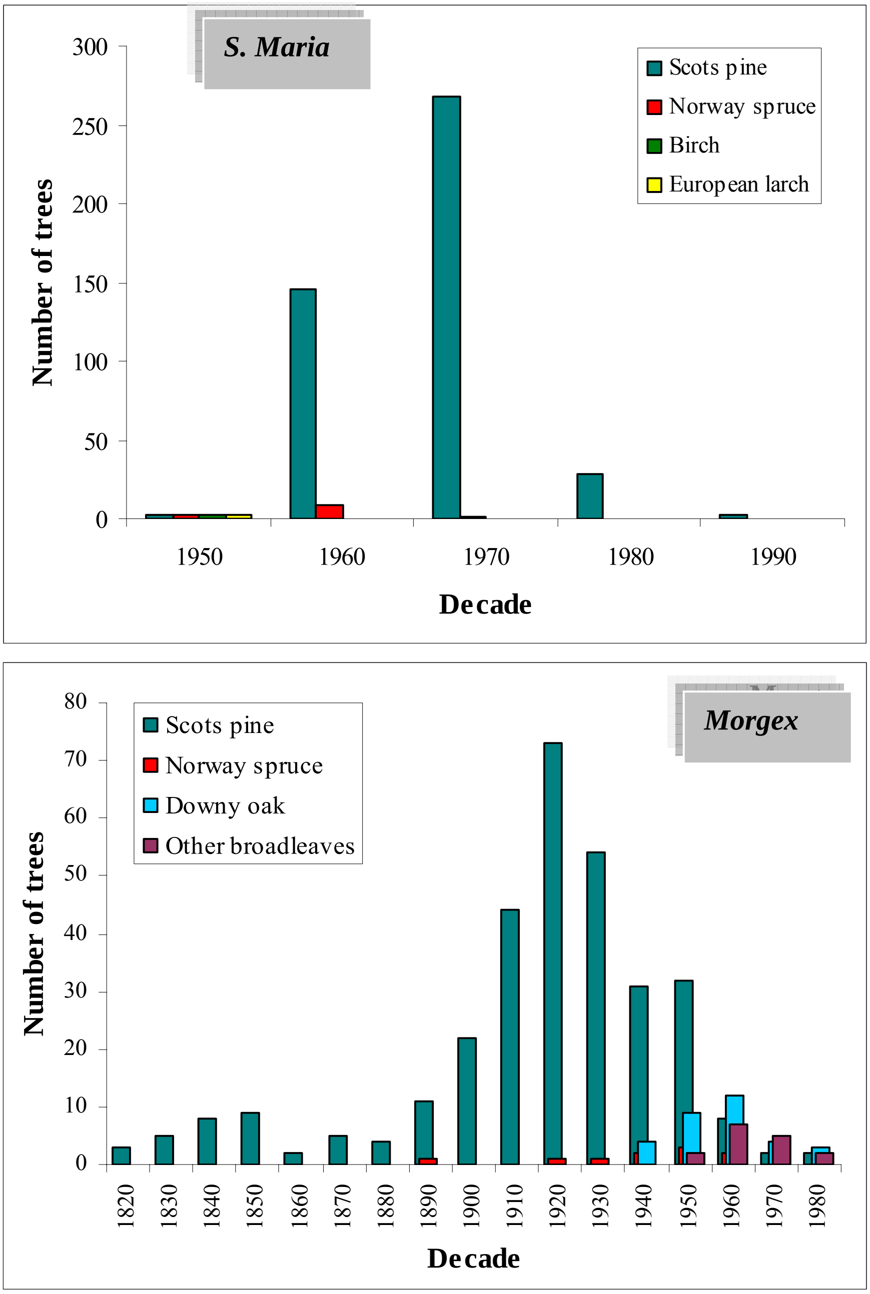
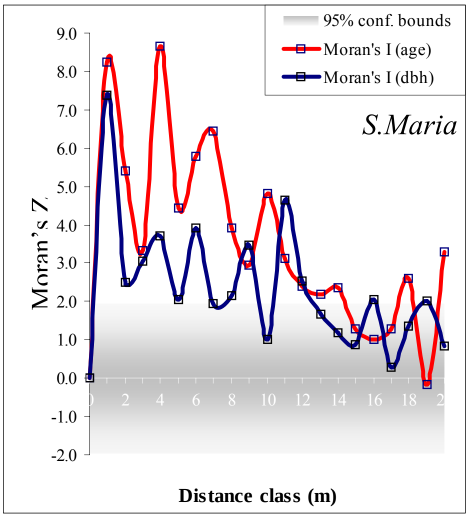
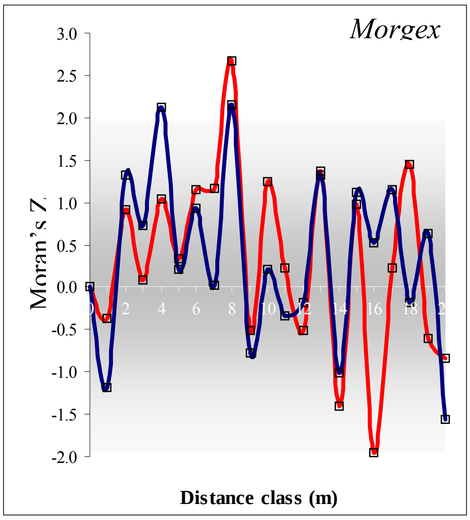
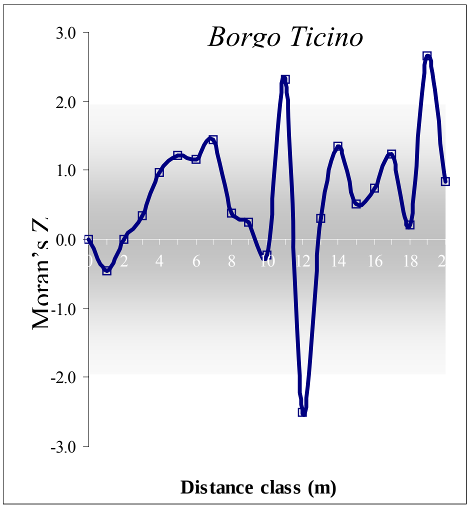
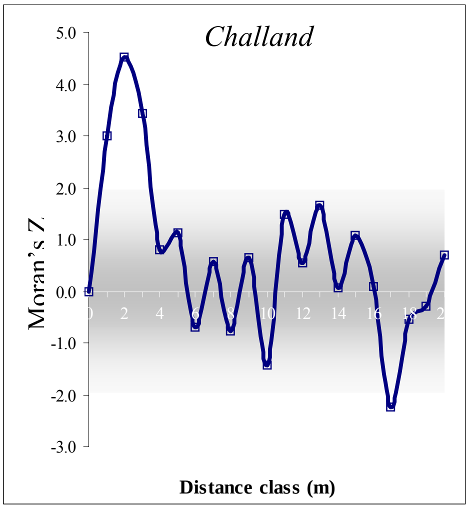


Figure 25 – Age structure of study areas, based on age at 50 cm height.


S.Maria
95% conf. bounds
Moran's I (age)
Moran's I (dbh)
Moran's Z
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
0
2
4
6
8
10
12
14
16
18
20
Distance class (m)


Morgex
Moran's Z
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
2
4
6
8
10
12
14
16
18
20
Distance class (m)


Borgo Ticino
Moran's Z
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
0
2
4
6
8
10
12
14
16
18
20
Distance class (m)


Challand
Moran's Z
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
0
2
4
6
8
10
12
14
16
18
20
Distance class (m)

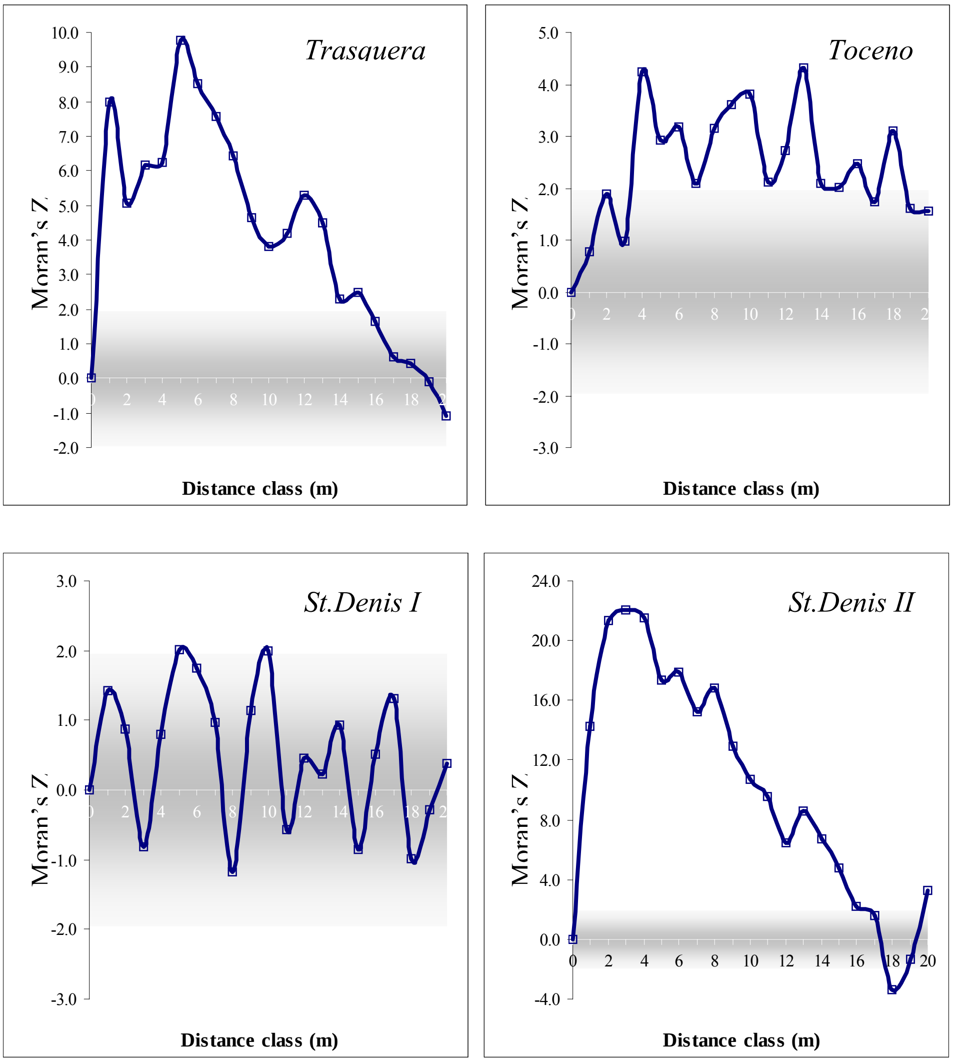


Figure 26 – Moran's correlogram for Scots pine dbh and age (where measured) in the study areas.

Analysis of tree growth patterns as a response to competition showed that while AGR was always positively related to tree size, RGR computed for the last 5 and 10 years decreased with an increase in tree size in S.Maria; RGR increased with tree size in the same plot when computed over 30 years, and in all cases in Morgex plot [Figure 27].

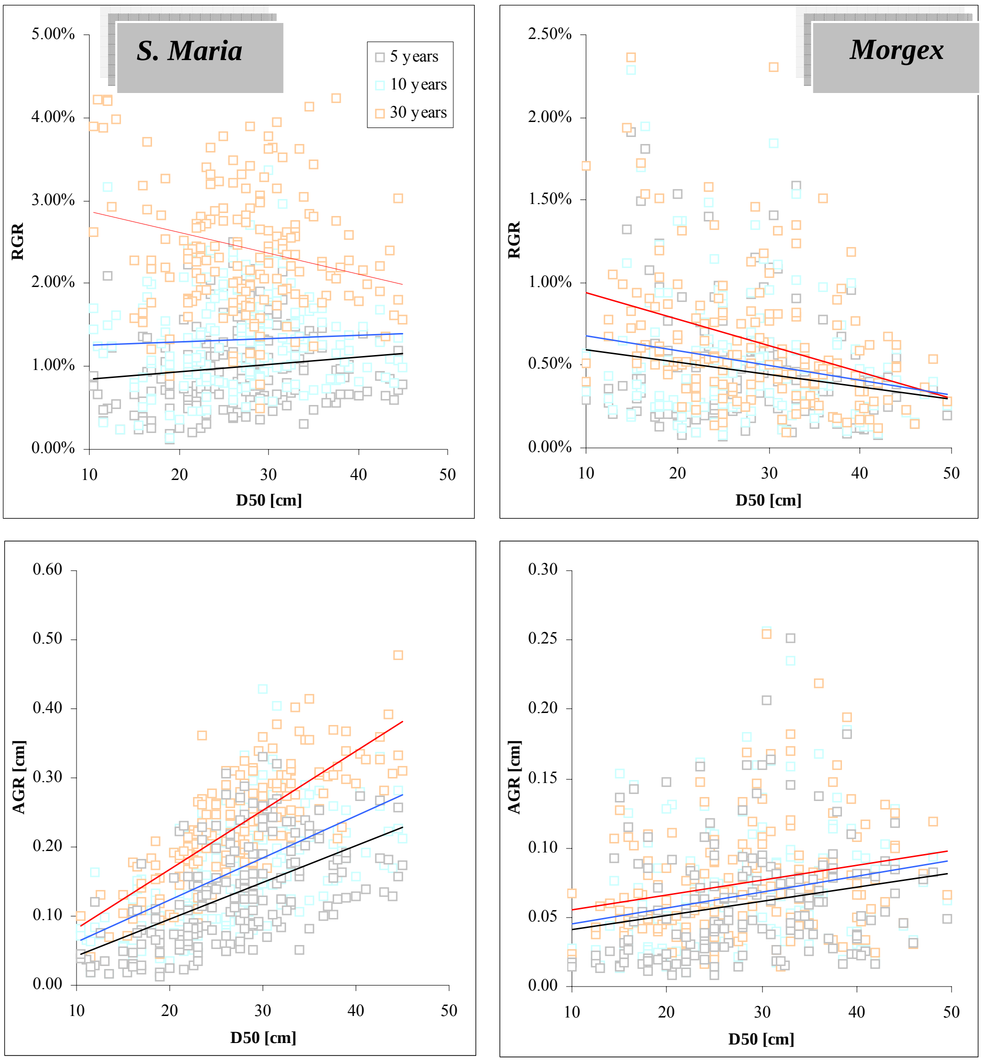


Figure 27 – Relative (above) and absolute (below) growth rate computed over the last 5, 10 and 30 years as a function of tree size in the study plots (data for focus trees and linear interpolations).

Computed competition indices for individual trees showed great variability. A selection radius of 10m usually resulted in higher coefficients of variation, and a radius of 5m in minimum variability. Indices such as CAI and CCS were characterized by wide ranges and extreme, isolated values; Daniels' and

Hegyi's indices, on the other hand, presented limited variability (CV between 0.44 and 0.78 for the latter mentioned). Most CIs are devised in such a way as to vary between 0 and +∞, showing higher values for a more intense competition. Exceptions are represented by Daniels' index, which behaves the opposite way, and Pukkala and Kolstrom's, which also takes into account negative competition, i.e., large trees have an effective advantage in growth [Figure 28].

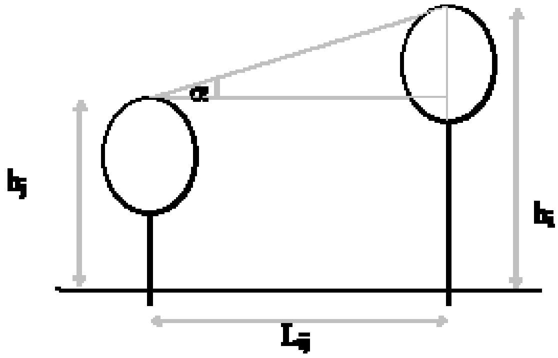


Figure 28 – Principle for Pukkala and Kolstrom competition index. α *is the vertical angle from the subject tree (*i*) top to the competitor (*j*) top,* h_i *is the height of the subject tree,* h_j *is the height of the competitor, and* L_{ij} *is the distance between the two. If the subject tree is higher than its* j*-th competitor, a negative quantity will be added to the* i*-th PK index (modified from Rouvinen and Kuuluvainen, 1997). PK values range from -∞ to +∞.*

The effect of competition on basal area growth is shown in Figure 29. The individual yearly and cumulative radial growth of focus trees experiencing minimum and maximum competition, as computed by the CI value, was compared with the stand-wide average for the two study areas. The higher steepness of cumulative increment curve in S.Maria witnessed more rapid growth in this plot at least for dominant trees (i.e., free from competition), while growth patterns of average and suppressed trees were comparable between sites. Moreover, growth series showed that dominant trees are able to adapt their growth pattern to exogenous dynamics (the spikes in dominant trees growth series correspond to the ones in the mean site chronology, and are imputable to yearly variations in climatic conditions). Suppressed trees, on the other hand, after an initial period of relatively sustained growth (competition may still be low at time of establishment), suffer limited increment for most of their growing period, even if they may show temporary releases.

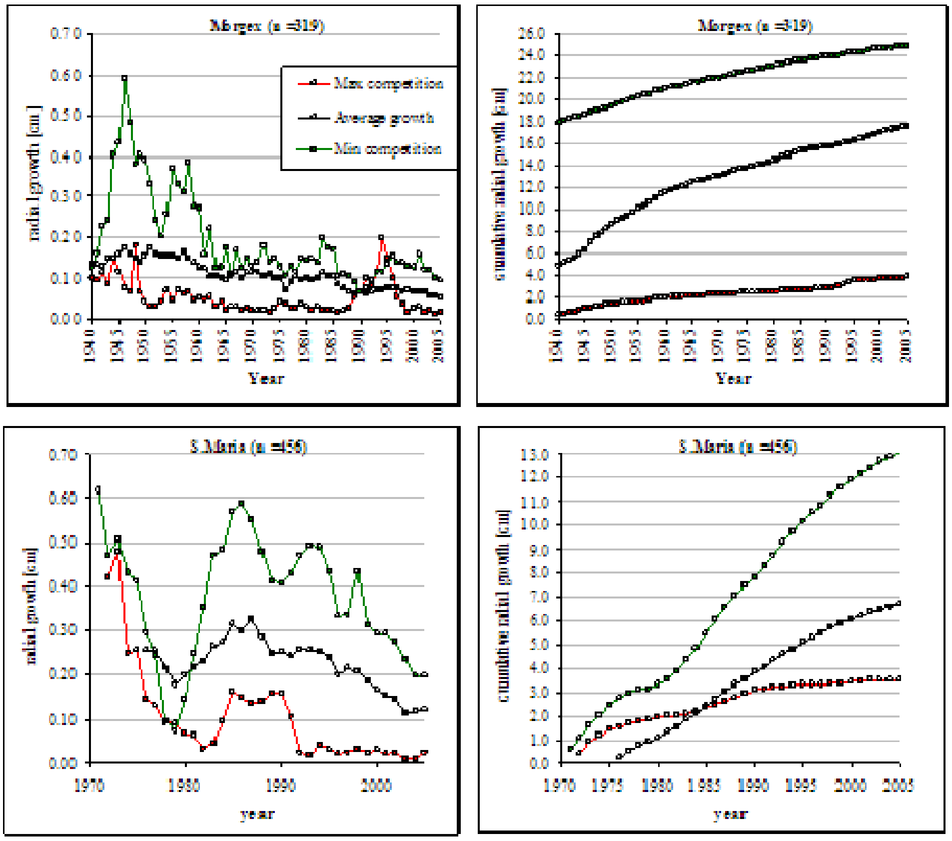


Figure 29 – Yearly (left) and cumulative (right) radial increments [cm] in the study areas. Graphs show the average site chronology (black) and the chronology of the tree suffering maximum and minimum competition (red and green respectively).

Moreover, neighborhood competition had an evident impact on tree survival and mortality, as can be seen by comparing the frequency distribution of Pukkala and Kolstrom's CI for standing live and dead trees [Figure 30]. A one-tailed t-test on both plots combined showed that average CI for snags was significantly higher than for living Scots pine trees (p >0. 95).

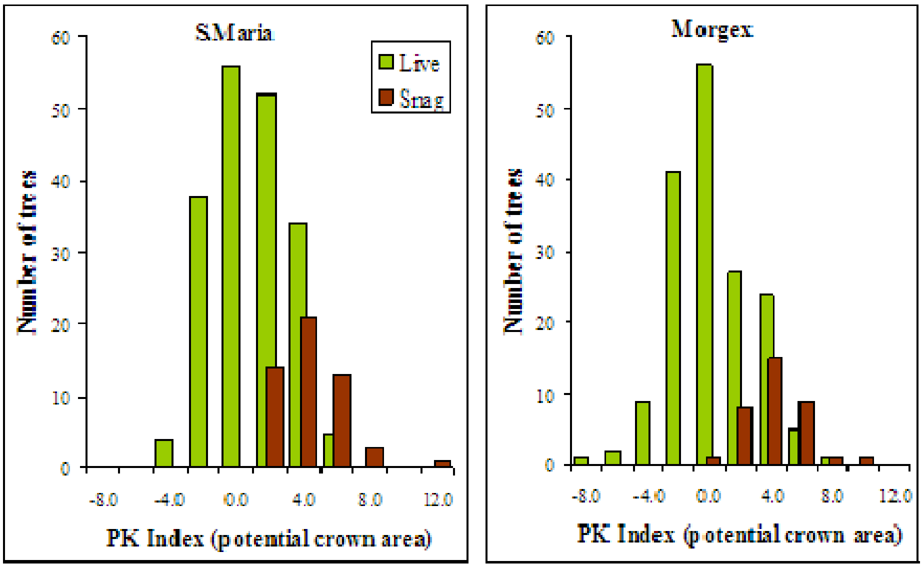


Figure 30 – CI distribution for living and standing dead trees in the study areas. Pukkala and Kolstrom index is coupled with the open-grown crowns competitor selection rule. A higher PK value means more intense competition experienced by subject individual.

Figure 31 shows that in the oldest plot analyzed, mature trees suffer little to no competition. In other words, surviving trees have for the most part already won the competitive struggle; this is in accord to expectations, since Scots pine is essentially an early-seral species and does not tolerate long suppression.

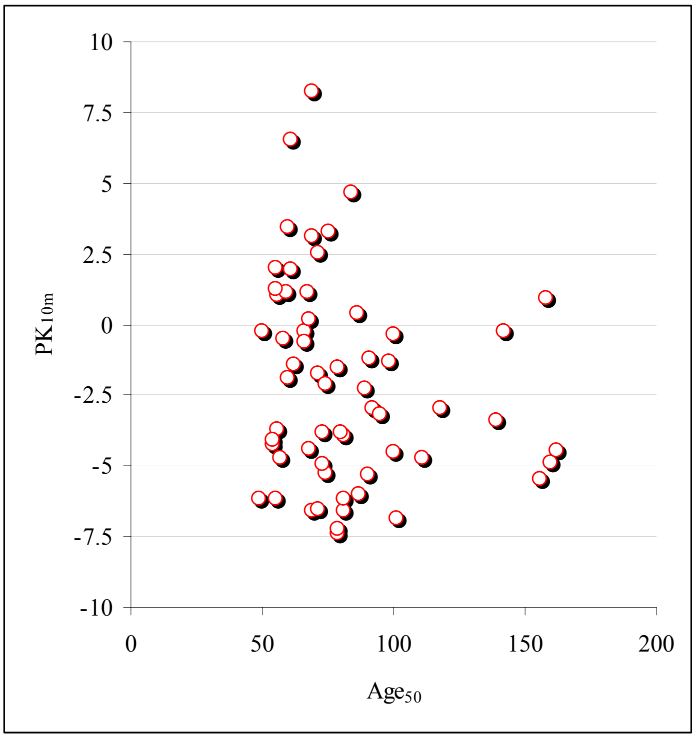


Figure 31 – Morgex: intensity of competition acting on trees of different age.

Table III.8 shows the performance of selected competition indices in terms of overall goodness-of-fit (adjusted R^2) for the logarithmic BAI model including tree size and CI as predictors [10]. The relationship was fit separately by plot, CI, increment period and competitor selection method. The model performed consistently better in S.Maria than in Morgex; the longer the time span analyzed, the more variation in target tree's BAI is explained. No selection method was universally superior to others, though the method based on influence zone overlap determined average to good results in S.Maria and worse results, as compared with other selection rules, in Morgex. In the latter plot, selection based upon a 5m fixed radius usually provided the best model performance.

Comp. Index		**S.Maria**			**Morgex**		
	Selection rule	*5m*	*10m*	*OCA*	*5m*	*10m*	*OCA*
Daniels	ln BAI$_{5}$	0.679	0.684	0.684	0.445	0.438	0.438
	ln BAI$_{10}$	0.714	0.716	0.717	0.470	0.463	0.464
	ln BAI$_{30}$	0.914	0.914	0.914	0.531	0.523	0.526
Hegyi	ln BAI$_{5}$	0.685	0.691	0.689	0.472	0.466	0.457
	ln BAI$_{10}$	0.725	0.723	0.726	0.496	0.491	0.482
	ln BAI$_{30}$	0.917	0.914	0.916	0.547	0.541	0.539
R.K.$_{1}$	ln BAI$_{5}$	0.680	0.681	0.681	0.446	0.446	0.445
	ln BAI$_{10}$	0.717	0.718	0.718	0.471	0.471	0.470
	ln BAI$_{30}$	0.916	0.916	0.917	0.533	0.533	0.533
R.K.$_{2}$	ln BAI$_{5}$	0.689	0.684	0.695	0.466	0.456	0.460
	ln BAI$_{10}$	0.728	0.716	0.733	0.488	0.479	0.483
	ln BAI$_{30}$	0.919	0.916	0.919	0.539	0.533	0.535
P.K.	ln BAI$_{5}$	0.706	0.713	0.711	0.550	**0.598**	0.558
	ln BAI$_{10}$	0.734	0.735	0.737	0.572	**0.618**	0.583
	ln BAI$_{30}$	0.916	0.916	0.916	0.581	**0.605**	0.594
CCS	ln BAI$_{5}$	0.723	0.718	**0.728**	0.448	0.448	0.449
	ln BAI$_{10}$	0.770	0.752	**0.774**	0.468	0.468	0.468
	ln BAI$_{30}$	0.927	0.922	**0.928**	0.527	0.527	0.527
CAI	ln BAI$_{5}$	0.685	0.680	0.685	0.440	0.440	0.439
	ln BAI$_{10}$	0.719	0.714	0.718	0.469	0.469	0.468
	ln BAI$_{30}$	0.918	0.915	0.916	0.514	0.514	0.514

Table III.8 – Goodness of fit (adjusted R^2*) for basal area growth model in the study areas. Model form is:* $\ln BAI_{periodic} = a_0 + a_1 \ln dbh + bCI$ *. The model was separately fit by study area, competition index (CI), competitor's selection method and response variable.*

The comparison between CIs demonstrated that the only non-spatial index used, i.e. Daniels', was associated with the worst performance in most model combinations. Increasing the relative weight of intertree distance (R.K.$_1$) or size ratios (R.K.$_2$) did not substantially improve model performance. Including asymmetry of competition into the model, on the contrary, was a good choice: the P.K. index, capable of accounting for positive as well as negative interactions, consistently resulted in higher model performance. The same result was obtained by computing competition based on crown areas (CCS), while combining the latter variable with tree height without accounting for competition asymmetry (CAI) proved not as good, especially where this index was biased by extreme, isolated values such as in Morgex.

Comparing the goodness-of-fit between the competition-inclusive model and a null model based only on focus tree's diameter[9], the highest improvements were provided when null model performance is lower (i.e. in the Morgex plot, with a 10m-radius selection rule) and consequently for the shortest increment periods. In such cases, inclusion of the best CI in the model explained up to an additional 16% of data variability. Additional variability explained by CIs in S.Maria plots ranged from 0% to 6% (improvement in adjusted-R^2); when 30-years BAI was considered, model improvement varied from 0% to 8% in Morgex and only up to 1.4% in S.Maria. RMSE improvement for the best combination of CI, selection rule, growth period and study area amounts to 6.66 cm^2 year^{-1}.

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[9] Null model: $\ln BAI_{periodic} = a_0 + a_1 \ln dbh$. Model performance (adjusted R^2) when growth period of 5, 10 and 30 years were considered was .673, .709, .911 and .434, .460 and .520 in S.Maria and Morgex respectively. RMSE ranged from 2.51 to 5.72 cm^2 year^{-1}; the lowest RMSE was associated to 30-years BAI in the S.Maria plot, but predictions based on 5- and 10-years growth performed worse than in Morgex for the same time span. All models were significant at the 95% confidence level (ANOVA F-test).

Model 1 [a,b] $\ln BAI_{30} = a_0 + a_1 \ln D_{50} + a_2 CCS_{OCA} + a_3 Age_{50}$

S.Maria	a_0	a_1	a_2	a_3	R^2_{adj}	**RMSE** [d]
Unstandardized	0.151 [c]	1.962	-0.018	-0.014	0.937	±60.81 cm^2
Standardized		0.890	-0.141	-0.070		

Model 2 [a] $\ln BAI_{30} = a_0 + a_1 \ln D_{50} + a_2 CCS_{OCA}$

S.Maria	a_0	a_1	a_2	R^2_{adj}	**RMSE**
Unstandardized	-0.129 [c]	1.897	-0.019	0.933	±62.13 cm^2
Standardized		0.861	-0.151		

Null model [a] $\ln BAI_{30} = a_0 + a_1 \ln D_{50}$

S.Maria	a_0	a_1	R^2_{adj}	**RMSE**
Unstandardized	-0.915	2.116	0.921	±69.12 cm^2
Standardized		0.960		

[a] All models significant at the 95% confidence level (ANOVA F-test).
[b] Collinearity diagnostics: VIF ≤ 5.3.
[c] Coefficient is non significant at the 95% confidence level (t-test)
[d] RMSE in cm^2 $year^{-1}$.

Table III.9 – Regression stats for best and null BAI_{30} model in S.Maria.

The full BAI model computed over the last 30 years shows optimal goodness-of-fit for the study area of S.Maria [Table III.9]; mean prediction error (RMSE) is quite high in both plots. Age at 50 cm height and competition index has been included by the stepwise routine in the full model in addition to tree size; these variables provided significant but limited improvement to the null model. Standardized coefficients are expectedly negative for both age and individual CI. Results in Morgex [Table III.10] show a worse overall goodness of fit and mean error prediction; inclusion of CI and age in the null model brought great improvements, explaining an additional 22.9% of data variability. The strongest negative effect on individual growth is played by age, which is responsible for a further 14% of total variance when added to the size-competition model. Analysis of the residual plots did not evidence any bias but a small overestimation of BAI under 25 years of age (S.Maria) and a small underestimation over 150 (i.e., a more limited variability in modeled increments as compared to observed growth).

Model 1 [a,b] $\ln BAI_{30} = a_0 + a_1 \ln D_{50} + a_2 PK_{10m} + a_3 Age_{50}$

Morgex	**a_0**	**a_1**	**a_2**	**a_3**	**R^2_{adj}**	**RMSE**
Unstandardized	0.782	1.525	-0.055	-0.011	0.762	±67.98 cm^2
Standardized		0.781	-0.322	-0.456		

Model 2 [a] $\ln BAI_{30} = a_0 + a_1 \ln D_{50} + a_2 PK_{10m}$

Morgex	**a_0**	**a_1**	**a_2**	**R^2_{adj}**	**RMSE**
Unstandardized	1.794	0.938	-0.067	0.622	±88.87 cm^2
Standardized		0.480	-0.391		

Null model [a] $\ln BAI_{30} = a_0 + a_1 \ln D_{50}$

Morgex	**a_0**	**a_1**	**R^2_{adj}**	**RMSE**
Unstandardized	0.336[c]	1.424	0.533	±97.43 cm^2
Standardized		0.732		

[a] All models significant at the 95% confidence level (ANOVA F-test).
[b] Collinearity diagnostics: VIF ≤ 2.4
[c] Coefficient is non significant at the 95% confidence level (t-test)

Table III.10 – Regression stats for best and null BAI_{30} growth model in Morgex.

Discussion

Stand dynamics

Each of the analyzed plots represents a unique situation, which is the result of site, climate, disturbances and land use factors interacting with each other. Relative density estimates for the study plots vary from 25 to 89 percent of the biological maximum represented by the self-thinning line (considering Scots pine only). According to Long (1985), a RD greater than 60% marks the onset of self-thinning, i.e., suppression and mortality due to competition. Two stands are close to this limit, and may be positioned in the zone of imminent competition mortality (Drew and Flewelling, 1979) if RD were computed on all species on the plot. Stands in S.Maria and in St.Denis are about to enter the phase of active self-thinning and mortality due to intraspecific competition; yearly mortality in S.Maria currently has a very high rate (26%), which suggests that self-thinning may already be in effect.

This stand established about 50 years ago on a former mid-alpine meadow. Remains of irrigation channels and stone walls can still be seen in the stand, as an evidence of the previous agricultural use of this land. Suchecki (1947) observed that self-thinning induced mortality in Scots pine stands of central Europe may begin at an age of 30-40 years (even sooner on poorer sites, i.e., at the age of 10-20 years) and usually peaks at 40-50 years. Kenkel et al. (1997) found the highest mortality rate in self-thinning *Pinus banksiana* Lamb. stands to occur between 30 and 35 years of age. Franklin et al. (1987) observed that the period of competition-related mortality occurs earlier and for a shorter period of time in tree species that grow and mature rapidly.

To confirm these findings, the size distribution of recent mortality is markedly different from the one characterizing live trees; mortality was found to involve mostly small-sized individuals, i.e., suppressed trees already suffering from competition of overtopping individuals. The canopy cover estimate (93%) corroborates the hypothesis of light being most limiting resource on this high-fertility site and regulating population density during self-thinning (Lonsdale, 1990). Progression of self-thinning dynamics in S.Maria is also shown in the relative growth rate plot [Figure 27]. When 30-yer BAI is taken into account, mean tree growth bears no trace of past competition: established saplings were free to grow below size-density thresholds for self-thinning, hence small trees show a greater vitality than older ones and a higher biomass production per unit size. On the other hand, in the last years competition-induced growth suppression and mortality began to play a major role. The resulting trend evidences increasing suppression of biomass production in smaller trees, while large (i.e., dominant) ones steadily maintain former growth rates.

The origin of the Toceno stand, located in close proximity to the former one, is unclear. Field evidence suggests that its origin could be similar to the younger stand, i.e., initial encroachment on grassland, with fire or intense logging possibly playing a role in stand initiation (Saponeri, 2006). Resin tapping scars suggest that the main cohort could be between 90 and 130 years old. This stand possibly represents a more advanced developmental stage, with increased tree size and decreased density due to prolonged self-thinning. Relative density is 89% of maximum SDI, meaning a protracted and intense influence of competition mortality on the stand. Yearly mortality is now around 2%, but this is not in disagreement with the previous statement: since QMD is so high, the mortality asymptote approximating the self-thinning boundary requires a small number of tree deaths to be maintained. Moreover, the stand could have been released from intense competition to a certain extent in the last years, when some of the mid-sized trees where logged by local users. Evidence of past competition can be found in vertical stand structure; self-pruning and crown uplifting were promoted by competition as can be seen from the low mean crown ratio characterizing the pine trees (Vacchiano, 2007c). Still, there is some growing space available to more tolerant species such as beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* Karst.) and silver fir (*Abies alba* Mill.). These late-seral component is now establishing as a shaded regeneration layer under the pine overstory (see Aussenac, 2002) and possibly represents both the future successional development and a further stable state of the stand (see also Chauchard et al., submitted). Most seedlings and saplings of these species, even when found in the field, where too small to be included in the measures; therefore, bivariate point pattern analysis does not evidence the expected aggregation pattern with the early-seral component (i.e., seedlings growing preferably under pine cover) but for quite large distances. An alternative explanation of this result could be found in the relatively high canopy cover (78%), which could prevent the ground from receiving enough radiation even for tolerant species, whose establishment could be spatially confined to mid-sized gap or less dense canopy patches.

It is generally accepted that the distribution of individual trees goes from clustered to random to regular as succession proceeds in natural stands (Cooper, 1961; Laessle, 1965; Kenkel, 1988; Chapin et al., 1989; Moeur, 1997; Stoll and Bergius, 2005). Spatial point pattern analysis in the previously mentioned areas suggests a similar process: when the stand is free from disturbances, Scots pine shows a regular or over-dispersed pattern at short distances (1-4 m). Following the encroachment phase, which could have led to a random spatial distribution since the seed source was external to the stand itself (Greene and Johnson, 1989), the onset of self-thinning caused an aggregated mortality, i.e., trees dying in clumps around dominant individuals (Kenkel, 1988). Surviving trees arranged in order to occupy available growing space in the most effective way, hence the over-dispersed pattern that can be observed at increasing distances. If self-thinning is allowed to proceed, the average intertree distance denoting a regular (nonrandom) pattern will increase together with the enlargement of tree size and competitive zone of influence.

Finally, the similarity between the two stands is confirmed by spatial autocorrelation of tree dbh (age), with the respective correlograms bearing a striking match to each other [Figure 26]. Pine seedlings established on fertile non-forested land; the establishment process on such a seedbed would happen in a quick way and without significant microsite limitations (Acherar et al., 1984; Booth, 1984; Lookingbill and Zavala, 2000; Castro et al., 2002; Dovciak et al., 2005; Chauchard et al., submitted). This resulted in a general trend of positive age autocorrelation, even if smaller even-aged groups are still recognizable in the correlogram. The average size of such patches (about 2 to 4 m) is extremely similar in both sites (compare also with Galinski et al., 1994; Kenkel et al., 1997; Kint et al., 2003; Rouvinen and Kuuluvainen, 2005).

Two other stands are located on high-fertility sites, but are representative of distinct situations. In Trasquera, the stand probably represents an old protection forest which was preserved from felling during the past centuries. A gap-opening phase can be distinguished, characterized by low absolute and relative densities (39%), well below the self-thinning threshold. Natural mortality of older trees and the impact of occasional felling during the last 20 years made some growing space available for a new cohort, which is establishing in dense groups in the gaps and gives the stand a distinct two-storied structure. It is unclear whether the stand has already gone through a self-thinning phase, the intensity of competition being later attenuated by tree removal, or if rather initial density was too low to trigger density-dependent mortality, whose recent evidence could not be found in the stand. The distance of this stand from the self-thinning boundary may also reflect Zeide's (1995) hypothesis that mortality of old trees exceeds lateral growth of crowns in overmature stands. This process results in a progressive accumulation of gaps as the stand gets older, so that the trajectory of stand development drops below the maximum density line.

A similar structure is common to the stand in St.Denis II, even if this one is located on a less fertile site (hence a much lower dominant height). Large patches of advance regeneration are present also in this stand, as can be seen from the bimodal size distribution. The higher relative density and lower gappiness of this stand, possibly due to lower stand age, did not prevent saplings from successful exploitation of local patches where high solar radiation could reach the ground. Sustained mortality rate must not be misinterpreted as a competition-induced effect: size distribution of recent mortality shows that mid-sized trees are more prone to die. As a matter of fact, the stand was impacted by a large blowdown that involved almost one third of standing basal area; both this event and occasional logging contributed to the stand's fairly open canopy.

In available literature, some studies suggested that regeneration of natural *P.sylvestris* forests is not significantly connected to gaps (Zackrisson et al., 1995), while in other studies a connection between regeneration recruitment or seedling growth and gaps has been documented (Kuuluvainen et al., 1993; Kuuluvainen and Juntunen, 1998).

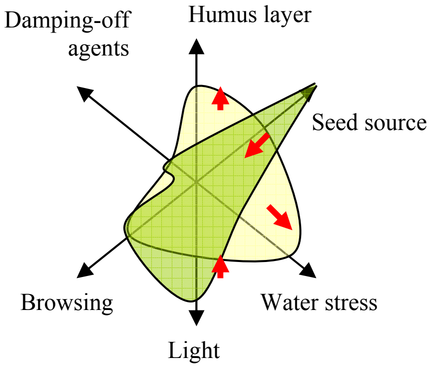
Spatial analysis on these two areas revealed a second common pattern. Pine trees are clumped on all distance classes up to 20 m, a pattern due to the presence of large regeneration patches. This pattern generates a high positive autocorrelation of dbh on short distances, attenuating as tree distance increases. In both plots, tree clumping was found to be significant at all distances, even if the absence of negative autocorrelation waves suggests that on larger distances trees of different age are more interspersed. No large patches of old trees could be found (even if the distribution of canopy gaps is the likely responsible for younger tree patches). The previously described stands are the likely result of a simultaneous regeneration wave and are characterized by the absence of pine new seedlings or advance regeneration. On the contrary, in Trasquera and St.Denis II the regeneration process is actively taking place under the partial cover of the residual, old overstory tree (two-layered phase). Permanence of Scots pine in the next generation is likely, even for lack of other regenerating species.

Stand history in Borgo Ticino is not as easily interpreted. Establishment of Scots pine on moorlands can lead to scattered patterns due to locally excessive moisture and unfavorable seedbed (Dimbleby, 1953; McVean, 1963; Agren and Zackrisson, 1990; Paavilainen and Päivänen, 1995; Coquillard et al., 2000; Prévosto et al., 2003) Stand density is approaching self-thinning more because of large mean tree size than because of density. No recent mortality has been found on site, and the overstory trees did not show any significant spatial pattern. Origin of the chestnut understory is not clear; the species shows an uneven-aged size distribution, but since the species does not play a role in typical vegetation of similar sites, this can be an effect of traditional selection treatments (irregular coppicing). After the abandonment of management practices, chestnut has taken hold of the understory; its repulsive pattern versus pines can be explained by mere spatial partitioning between a mature overstory and a young and dense understory. Pine regeneration has no chance of finding suitable sites due to the full cover of the two canopy layers; the site is not much suited for chestnut too, but the former coppice will have to undergo a phase of self-thinning before other climax species such as oaks could re-establish. As an alternative, a stand-replacing fire could easily occur due to the abundance of dry leaves and fuel ladders provided by chestnut; in such a case, Scots pine seeds could be the fastest in colonizing the site (McVean, 1963; Sannikov, 1994; Schimmel and Granstrom, 1996, 1997; Linder, 1998; Nunez et al., 2003; Hille and Den Ouden, 2004; Hancock et al., 2005).

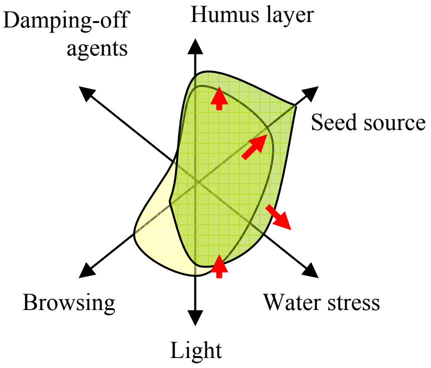
Scots pine cover is referenced as continuous in the last centuries for the Morgex (Saponeri, 2006) and Challand sites, either due to site limitations or to intensity of management that kept the stands open enough for adequate regeneration of early-serals. Now that management is likely to be much less intense, in both stands we observed an increasing broadleaved component. In both cases, some trees have already reached the upper canopy layer; mortality of small pines on the sites may be therefore due to increased interspecific competition. This would agree with RD levels on the plots, not high enough to justify self-thinning when only growing space for pine is taken into account. Small-scale, continuous (or wave-like) establishment is confirmed by the shape of size distributions, especially in Challand, and by the wave-like autocorrelation patterns. Even if the wide range of represented sizes and the consequent low consistence of samples from each dbh class may hamper the significance of Moran's index, positive and negative autocorrelation maxima may be related to small, even-aged patches developing in different times and places in the stand, likely due to episodic felling.

A small amount of yearly and recent mortality has been found in both plots, but it is unclear whether this be due to increased competition intensity caused by exploitation of growing space and belowground resources by broadleaves, or rather to small-scale disturbances acting in the stands (e.g., endemic pathogenic infections on individual trees). It is possible that the two processes happen at the same time; anyway, analysis of species composition stands for a prevalence of disturbance-induced mortality in Challand (high incidence of early-seral species in the broadleaved component, clumping of pines at all distances presumably due to large gaps). On the opposite, the presence of a quick growing downy oak component in Morgex may suggest an increase in competition levels acting on Scots pine, due to the life traits of the two species [Figure 32]. Positive spatial association between oaks and pine was found in St.Denis I for all distances, but also in Morgex Ripley's $L_{12}(t)$ showed an aggregation maximum at t = 4m (even if statistically non significant, data not shown).

Success of Downy oak regeneration has been associated with elevations of 1000 to 1200 m a.s.l.m. and with the co-occurrence of dry seasons, mid to high overstory density and thick humus layers (Rigling et al., 2006), all conditions actually realized in the Aosta Valley study areas. Braun-Blanquet (1961) already stated that most pine forests at lower elevations must be regarded as degradation stages of *Quercus pubescens* woods; extensive repeated sampling in the framework of the Swiss National Forest Inventory evidenced a significant shift from pine toward oak-dominated forests (Rigling et al., 2006). Overall basal area occupied by pine decreased by 12.7% in the last 20 years (-23.5% aon elevations lower than 1100 m a.s.l.) (Rigling et al., 2006); a landscape-wide shift in forest composition was confirmed by analysis of aerial photos by Tinner (2004). The time required for the successional shift is referenced to range from 80 to 140 years (Hadorn, 2003; Kienast et al., 2004; Rigling et al., 2006). In the patterns of vegetation dynamics described for the Mediterranean Basin (Quézel and Barbéro, 1990; Barbéro et al., 1998), *Pinus* species are considered pioneer species in succession, which are usually replaced by mid-successional *Quercus* species. In this framework, mixed forests are usually considered as a successional stage of initial post-disturbance pine forests. Even for mountain forests, it has been hypothesized that the observed ingrowth of oak in mountain forests previously occupied by pine can be regarded as a succession towards the potential natural vegetation after a century-long history of disturbance favoring the early-seral pine (Rigling and Cherubini, 1999; Lookingbill and Zavala, 2000; Lock et al., 2003; Kienast et al., 2004; Rigling et al., 2004; but see Bendel et al., 2006). Simulations performed in a disturbed homogeneous landscape or in heterogeneous landscapes indicated long-term co-dominance of both species (Zavala and Zea, 2004) [Figure 33]. Global warming scenarios predicting increased drought in the winter and spring season, when emergence of pine seedlings is to occur, envisage a further decrease in the pine component of such woods. These predictions agree with the light-water tradeoff hypothesis (Tilman 1988; Smith and Huston 1989) which states than final stand composition in the upper end of an aridity gradient is driven by tolerance of shade.



Pinus sylvestris



Quercus pubescens

Figure 32 – Optimal conditions for pine and oak regeneration (green) compared with actual situation in low elevation forests (yellow) and future tendencies (from Rigling et al., 2006). Displacement between current and optimal conditions is more pronounced for pine and is predicted to increase even further. Relative tolerance of pine and oak to drought may vary between the germination and development stage and between seedlings and adult individuals; literature is controversial about this issue (e.g., Zavala and Zea, 2004).

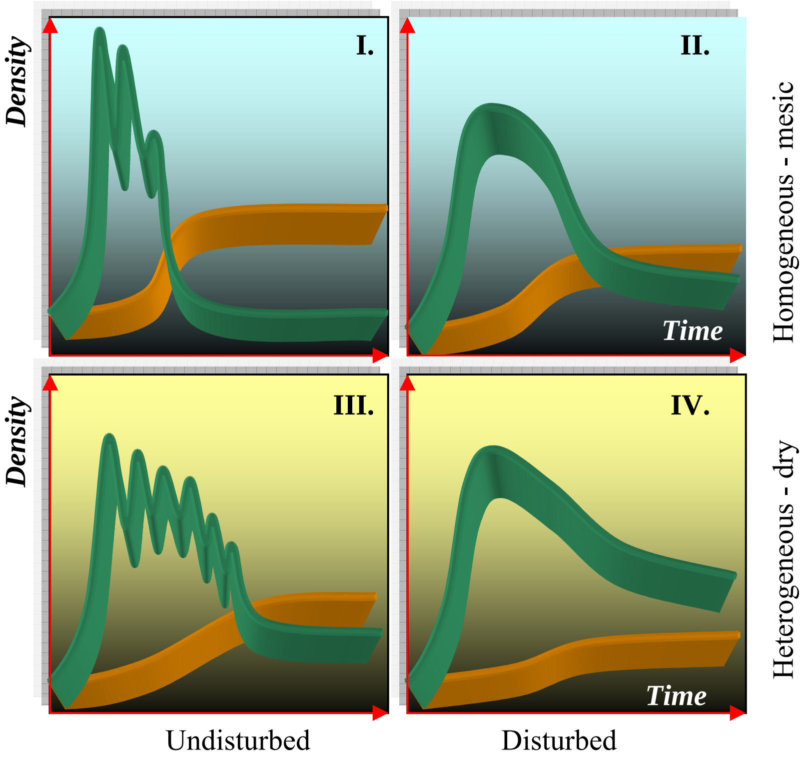


Figure 33 - Temporal variation in pine (green line) and oak (orange line) density as a function of site moisture and disturbance regime (from Zavala and Zea, 2004).

I: In mesic, undisturbed environments, Pinus' wider regeneration niche allows rapid occupation of an empty landscape reduced light levels under the pines *ameliorate water stress on oak seedlings (Retana et al., 1999), possibly facilitating their establishment (Lookingbill and Zavala 2000). In the long run oaks outcompets pines because of their saplings' greater tolerance of shade.*

II: in disturbed mesic homogeneous landscapes, pines are competed locally but their long dispersal tail and high seedling survival rates, relative to oaks, may allow them to capture open sites and persist in the landscape as fugitive species (Horn and MacArthur, 1972; Levin, 1974; Hastings, 1980). Oaks advance, gradually forming clusters that disappear in the long term if genets are killed by disturbances.

III: In the drier end of an aridity gradient the benefits of partial shade provided by pines may no longer compensate for the costs of water competition. Therefore in these sites, pines compete oaks by tolerating lower water levels and can form monospecific stands that follow autosuccesional dynamics.

IV: In heterogeneous disturbed environments, arid patches may have a critical importance for guaranteeing species diversity. During periods of low disturbance rates such as suppression of agriculture, silviculture or fire, oaks gradually displace pines, which remain confined to the most arid locations. If the disturbance regime changes as a result of climate-driven events or land use changes, these local refuges provide seed sources that allow pines to invade disturbed areas and expand their realized niche.

A consistent trend is shown by RGR analysis in Morgex: self-thinning has not set on the totality of stand area, but the last years marked an increase in competition intensity resulting in decreased steepness of the RGR lines. This shows that competition has been playing a major role only in the last few years, accompanying the abandonment of management practices and the increase in interspecific concurrence due to broadleaved invasion. The results suggest that RGR can be used effectively to derive conclusions on the competitive status of a forest stand (Larocque, 2002).

Examination of age autocorrelation helped in reconstructing past establishment mode of pines in different ecological situations. Figure 34 shows the three models developed for stand establishment and consequent dynamics for the described plots, portraying simplified Moran's correlograms. In complex stands, the existence of different species and different tree sizes constitutes confounding factors that can hinder the interpretation of the spatial structure if all the trees are considered. Trees present various degrees of competitiveness which depend on their species but also on their size: the bigger a tree is, the more competitive it is (larger crown and larger root system). The spatial structure of the pine trees alone proved easier to interpret as it is directly linked to regeneration dynamics and post-recruitment intraspecific competition (Moravie and Robert, 2003), while bivariate spatial patterns helped in detecting interspecific patterns relating to competitive displacement, facilitation and succession between species.

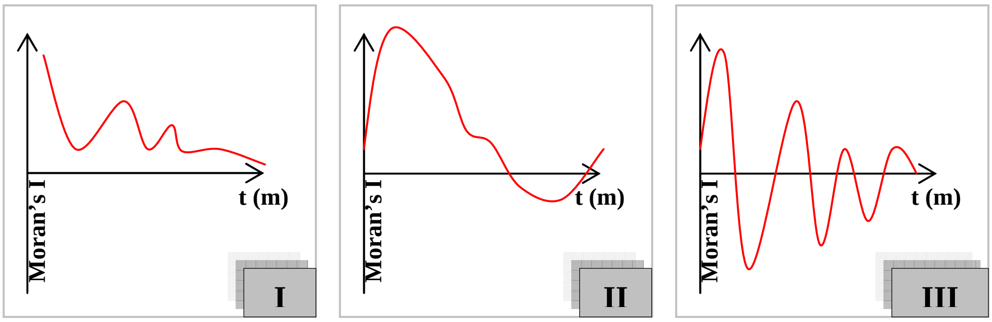


Figure 34 – Conceptual models for stand establishment and successive dynamics, represented on Moran's correlograms. I: Secondary invasion of non-forested land; uniform establishment and successive competition effect. II: Large seedling patches establishing under big gaps in the mature tree cover (stand re-initiation stage according to Oliver and Larson, 1996). III: Mid- to small-scale establishment with spatio-temporal heterogeneity due to patchy disturbance events.

St.Denis I, on the other hand, represents a unique case: extreme mortality rates are associated with a low relative density, but the size distribution of mortality does not show any difference with respect to living trees. No evidence of past management was found on this site; therefore, the low RD might be due either to low site fertility hampering successful establishment (as confirmed by dominant height) or to subsequent density-independent mortality, evenly reducing pine density in all size classes. Clumping of live and dead pines was found at all distances, as a legacy both of establishment pattern and of subsequent disturbance events. The contemporary establishment of downy oak (comparable dbh distribution) was characterized by an aggregation pattern towards Scots pines, imputable either to the ecological characteristics of the species (Ellenberg, 1988; Tonioli et al., 2001; Kunstler et al., 2005) or to poor site conditions, shallow soil limiting the spatial availability of adequate growth sites. An aggregative pattern of mid-successional oaks towards pines is in accord with available literature dealing with Mediterranean ecosystems (Espelta et al., 1995; Lookingbill and Zavala, 2000). Past researches explained this pattern with the facilitative action of pine overstory towards oak seedlings, more demanding in light and moisture after germination, especially during the dry season. Eilmann (2006) and Weber et al. (submitted), on the other side, argued that Downy Oak may exhibit a higher degree of drought tolerance as compared with Scots pine. Additional research is needed to this regard in order to assign existing stands to the correct successional model.

The interference caused by exogenous disturbances in successional development of pine forests may also be noted by spatial pattern analysis. In St.Denis I, Moran's correlogram does not evidence the typical fading of the autocorrelation signal with increasing distance (Legendre and Fortin, 1989). Even if the index is non significant for its most part, this shows that an establishment pattern of type I [Figure 34 – Colonization of abandoned non-forested land] was modified by subsequent events. Disruption of the establishment-determined pattern of pines is not imputable to competition, which at the moment is not intense as shown by the low RD value. Data from health assessment (Dobbertin et al., unpublished data) and field recognition evidenced the biotic origin of disturbance factors in the stand. High incidence of mistletoe (*Viscum album* L.) infections, blue stain fungi (Nicolotti et al., unpublished data), Pine processionary moth (*Traumatocampa pityocampa*) and Pine Shoot Beetle (*Tomicus piniperda*) repeated attacks (data from management plans) mark as uncertain the future persistence of pine in this area [Figure 35].

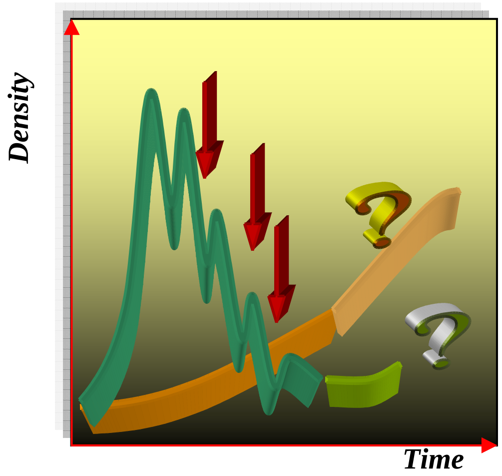


Figure 35 – Modification of successional pathway for mixed pine-oak stands in heterogeneous, arid sites (rainfall in St.Denis: 450 mm year^{-1}*) as a consequence of epidemic, pine-specific decline agents. Oak density is expected to increase should pine decline free additional growing space. Quantification of the impact of each agent on pine survival is needed to make meaningful predictions.*

Size distribution analysis provided more detail about the processes underlying competitive interactions. Any resource-mediated competitive interaction among individual plants can be placed somewhere along a continuum between completely size symmetric competition, where resource uptake among competitors is independent of their relative sizes, and completely size-asymmetric competition, where the largest plants obtain all the contested resources (Schwinning and Weiner, 1998). Size inequality in a population is considered the outcome of asymmetric competition (Hara, 1988; Yastrebov, 1996). A certain degree of initial size heterogeneity may appear because of genetic heterogeneity (Bonan, 1988), microsite or spatial heterogeneity (Weiner, 1985), and seed heterogeneity (Westoby and Howell, 1986). When trees rapidly encroach on a new site, the new stand usually tends to a fairly homogeneous size distribution (Rouvinen and Kuuluvainen, 2005). After crown closure, increasing competition for light may favor the bigger individuals, which grow disproportionately more than smaller ones (Wilson, 1988), thus increasing size differentiation and promoting a positively skewed (L-shaped) size distribution (Mohler et al., 1978). With the onset of self-thinning, the smallest individuals are outcompeted and die, leading back to a more homogeneous size distribution shifted to an higher dbh (Knox et al., 1989; Kenkel et al., 1997). The establishment of a new cohort later on results in a marked size heterogeneity [Figure 36].

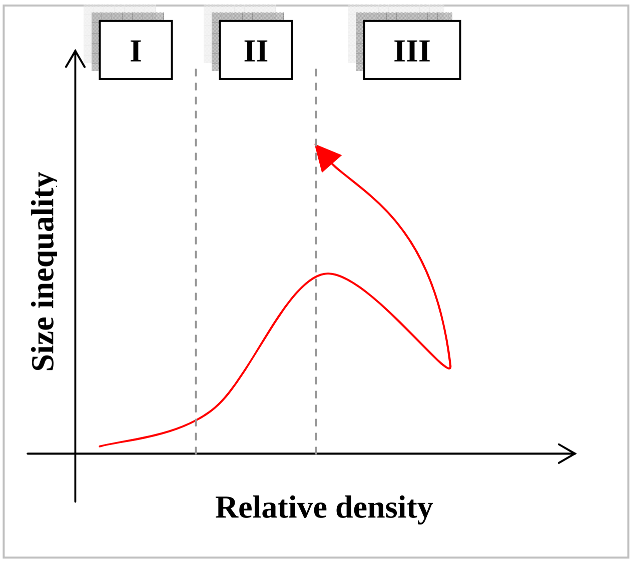


Figure 36 – Conceptual model for development of size hierarchies in pure, even-aged stands establishing on non-forested sites. RD zones associated with

(I) free growth, (II) suppression and (III) self-thinning are marked on the graph. The path and ending point of the last segment (stand reinitiation) is largely dependent on species, site and disturbance events; big leaps in size heterogeneity may be triggered even by a small initial amount of regeneration under the previous canopy.

The analyzed sites partially reflect this conceptual model. St.Denis I, Morgex and Challand are located on an increasing trend of RD and inequality (Gini coefficient) before the onset of self-thinning. The latest two likely have higher inequality than predicted by the simple trend proposed herein, since they are the result of spatio-temporally prolonged establishment rather than secondary colonization of available growing space. S.Maria is located on the decreasing inequality line (density-related mortality is already in effect), while Toceno shows even lower size differences once self-thinning has been continuously affecting tree survival. Trasquera and St.Denis II are good examples of two-layered structure, showing different RD level – imputable to different disturbance intensity and pattern – but almost same inequality, which can be thought of as a species-specific feature of regenerating stands. The stand of Borgo Ticino does not follow the proposed trajectory because of its peculiar structure, composition and history; the high site fertility (see dominant height) may also have played a role in reducing the impact of individual size differences of trees most likely established in a scattered way (and thus never undergoing severe competition, as could be inferred on the field from residual trees' deep crowns and thick branches).

Tree-scale competition

Competition indices have been used to evaluate two different components of the competition process: intensity and importance (Welden et al., 1988). The intensity reflects the absolute severity of the physiological strain induced by competition; it is independent of the intensity of the other factors affecting the performance of individual trees. Intensity is identified with the slope of a linear model. The importance of competition refers to the relative degree to which competition determines the physiological status or fitness of the individuals, the population growth rate, or community structure (Welden et al., 1988); it corresponds to the coefficient of determination of the model.

Both the partial and the full BAI models including competition measures showed that competitive dynamics have a high importance in influencing pine growth in S.Maria, where the higher site fertility does not represent a limiting factor for individual increment.

However, standardized coefficients for CIs showed higher competition intensities in Morgex, most likely due to the older age of the stand and the higher heterogeneity of individual tree size (see Gini coefficient, Table III.5). Older trees usually mean bigger trees, at least in the upper canopy layer and for an intolerant species like Scots pine; bigger, older trees determine in suppressed individuals growth reductions that are higher in magnitude than the ones caused by more homogeneous and smaller competitors (S.Maria). As noted by other studies, intensity and importance of competition are not necessarily related (Atkinson and Shorrocks, 1981; Shorrocks and Rosewell, 1987; Welden and Slauson, 1986).

The action of regulating factors unaccounted for (i.e., local site variability or disturbance agents) is shown by the lower goodness-of-fit of all model combinations in Morgex. Here, competition is only locally intense and spatially heterogeneous in the stand; including CIs in size-based growth models brought significant prediction improvements, especially when BAI is evaluated over a small amount of years and hence is more subject to yearly variability (from climate or other sources).

In S.Maria, even inclusion of the best CI did not improve much the performance of the null size-based model. Individual growth differences are well explained by size variability; growth predictions are reliable also on low time spans, since growth is fairly uniform from year to year due to young stand age and moderate influence of exogenous factors (see mean site chronology in Figure 29).

High fertility and younger age in S.Maria produced higher absolute BAI as compared to Morgex, but the same factors may also be responsible for the higher mortality rates in the former study area. The discrepancy between information implied by RD estimates (i.e., mortality as the competition effect) and assessment of competitive intensity/importance is explained by the complex interrelationship between stand history, individual heterogeneity, survival and site fertility (White, 1981; Goldberg et al., 1999; Morris, 2002). We conducted a qualitative assessment of the fertility/competition/mortality interactions according to the following alternate models:

I. Trees grown on fertile sites may mobilize resources at a fastest rate, being therefore more sensitive to moderate resource depletion determined by the presence of neighbors. On the opposite, limiting sites may activate adaptive responses in trees, which may therefore tolerate more severe growth reductions without dying as a result of suppression (i.e., exhibiting a more plastic response). A literature review on this topic evidenced both support (Boerner, 1984; Grubb, 1985; Tilman, 1987; Niinemets and Lukjanova, 2003; Dehlin et al., 2004) and disagreement (Grime, 1973, 1979; Weiner, 1985; Gurevitch et al., 1990; Donohue et al., 2000; Niinemets et al., 2001; Ladd and Facelli, 2005) to this hypothesis, which should in any case be tested species-wise. Such ambiguity has likely risen due to confusion between competitive intensity, effect and response (Grace, 1995; see also Introduction) or to choice of a different response variable to assess competition intensity (Ladd and Facelli, 2005).

Higher mortality has been related to better productivity by, e.g., Yao et al. (2001), Eid and Tuhus (2001), and Jutras et al. (2003) for Scots pine. Vanclay (1994) has expressed criticism of this relationship, because, in principle, good sites are expected to support higher stocking than low-productive sites. We hypothesize that site fertility affects not only the time required to the stands to develop over its size-density trajectory (Sukatschew, 1928 cited in Yoda et al., 1963; White and Harper, 1970; Bi, 2004) but also individual response to competition (i.e., plasticity vs. mortality) and the maintenance of size heterogeneity throughout stand development (Morris and Myerscough, 1984; Nilsson et al., 2002). As shown by Figure 37, competition can be thought of as a mediator between site characteristics and growth and mortality response of the stand, either in a direct relationship or through the differences in individual size hierarchies.

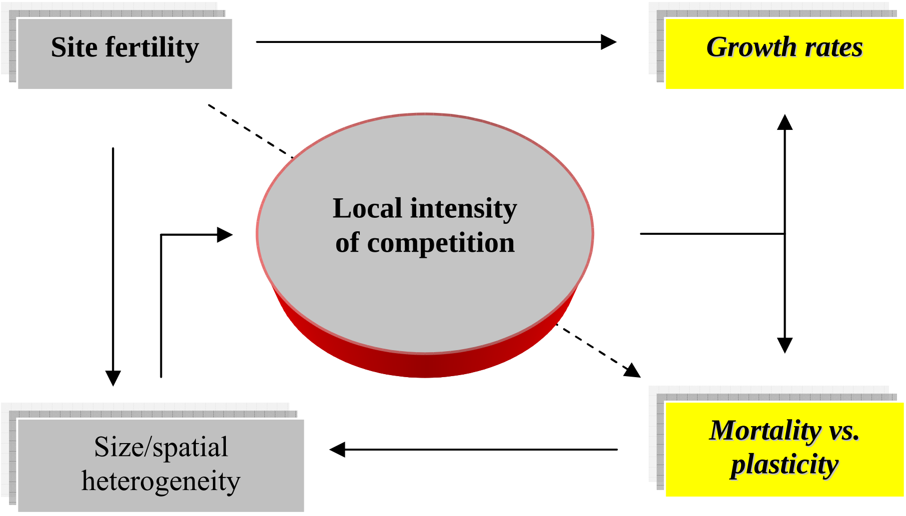


Figure 37 – Relationship between resource availability, individual heterogeneity and tree response as mediated by competition. If fertility is low, a positive feedback is triggered through the activation of plastic response, the maintenance of higher size inequalities and the promotion of local competition intensity, which slows tree growth and stand development. When more

resources are available, mortality is the mediated response and the stand can quickly proceed through subsequent structural stages. Survival and growth response can be considered uncoupled (Matthes-Sears and Larson, 1999). This model is supposedly applied to early-seral species dynamics.

II. Individual response in plasticity/mortality equilibrium (Sorrensen-Cothern et al., 1993) may rather be mediated by the age structure of the stand. On one hand, higher fertility promotes faster attainment of mortality-inducing competition levels, as previously stated. Lower mortality rates, even in the presence of higher competitive intensities at the local scale, may be imputed both to a time lag in crowding-induced mortality due to lower growth and biomass accumulation rates when nutrients are scarce (Westoby, 1984; Morris, 2003), and to the higher mean tree size of the Morgex stand, which requires more modest mortality rates than the younger stand in S.Maria to maintain its RD level.

  Moreover, younger stands naturally exhibit a higher homogeneity between individuals, that respond to competition via intense scramble and higher mortality rates (stem exclusion). Older stands have already undergone some structural differentiation; here, individuals may respond to competition in a more plastic way,. i.e, surviving to even more drastic growth reductions thanks to higher amounts of stocked carbon and slower response to disturbing factors (Berger et al., 2004). Evidence of age structure mediated competitive effect is provided by the importance of Age as a BAI predictor in the models. This reflects both local variation in dominance (Scots pine being a typical early-seral species with good association between age and size) and the more complex structure of the Morgex stand as compared to the younger one, where age is fairly constant among all individuals and does not play a significant role in predicting differences in growth.

III. The type of limiting resource involved by the competitive struggle (e.g., light, water or nutrients) further differentiates both the intensity and the effect of competition. Differences in resource types may determine the activation of alternative competition modes (resource pre-emption vs. depletion, Schwinning and Weiner [1998]) and symmetry between individuals or species (Fahey et al., 1998), further altering the described conceptual models (Wilson, 1988; Morris and Myerscough, 1991; Schenk, 2006). Previous researchers found a direct relationship between increasing site productivity and competition asymmetry (Keddy et al., 1997, 2000). It has been reported that symmetric competition leads to a type of stagnation, in which plants stop growing but do not die, whereas asymmetric competition (dominance/suppression model) results in growth of some plants and death (self-thinning) of others (Weiner, 1985; Yastrebov, 1996). In such a case, size inequalities would develop at a faster rate as competition becomes asymmetric (i.e., for light) and a few large individuals gain dominance and suppress many small ones; if suppression is severe, it can lead to a proportionally higher mortality of small individuals and, as a result, re-normalize the population size structure (Weiner and Thomas, 1986). Previous studies have shown that size inequality lessens when nutrients become limiting (Weiner, 1985; Creed et al., 1997) and natural variation in individual growth rates becomes less expressed (Turner and Rabinowitz, 1983). In such case, the stand in S.Maria is to be considered to have already overcome the mortality-induced normalization point, since its asymmetry is less pronounced than in Morgex.

Testing of alternative models, of competition mode (symmetric vs. asymmetric) and of the influence of exogenous change factors (e.g., climate shifts, insect or fungal impacts), must be sought by detailed studies, implying local measures of competition (Shi and Zhang, 2003) and possibly linking stand dynamics to individual physiological responses by means of hybrid modeling (Milner et al., 2003; Valentine and Makela, 2005).

The described interactions also imply that comparisons of intensity/importance of competition across sites, species or across different studies, are quite meaningless if the influence of resource availability is not taken into consideration. Basal area modeling is not the main focus of the present research; hence, the high RMSE values presently do not represent a relevant concern. Anyway, a better control of regulating factors and possibly more performing statistical model forms should be sought if growth prediction accuracy was the main objective.

In several studies, regression coefficients computed between BAI and different competition indices varied from low to high in absolute values, even using the same data sets. In the present study, when only CIs were considered as predictors, the tree size-related variable implied in all of them always produced a strong association with individual increment [Figure 38].

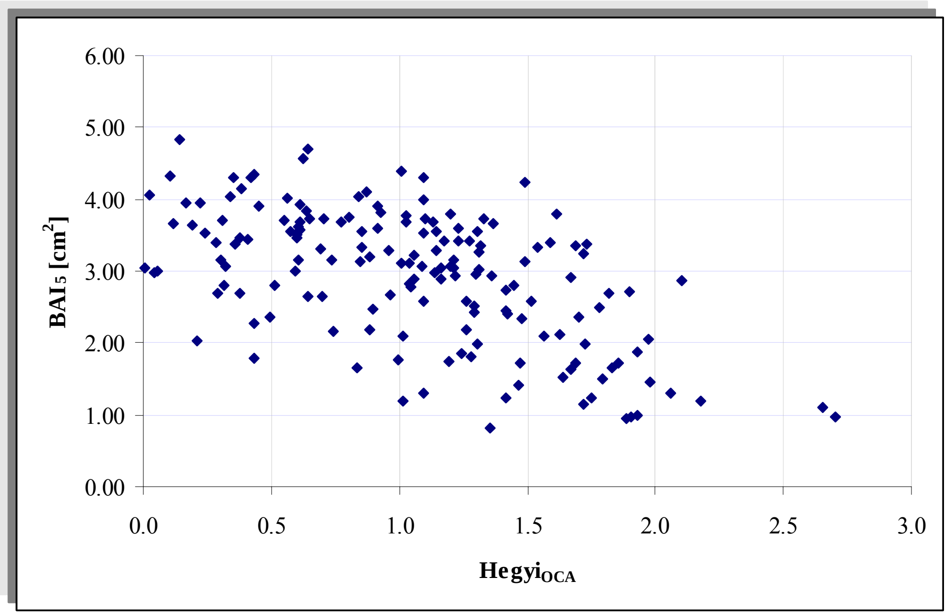


Figure 38 – Relationship between 5 year-BAI and Hegyi's CI in the Morgex area. Even with great variability in individual increment and competitive conditions, a simple index incorporating focus tree's size shows good correlation to individual growth.

Holmes and Reed (1991) noted that the good performance associated with competitor-to-subject's dbh ratios can be explained by the correlation existing between subject tree's diameter growth and its dbh, which is included is most CIs directly or as a correlated variable – i.e., subject tree's height or crown size are usually well predicted by diameter (Lappi, 1991; Niklas, 1994; Hasenauer, 1997; Grote, 2003; Mehtätalo, 2005; Diéguez-Aranda et al., 2006). Analysis of null competition models evidenced that diameter alone has a good relationship to individual tree growth (see also Kikuzawa, 1999).

The inclusion of tree size in individual-tree models has been justified on the grounds that initial size accounts for previous growing conditions and genetic inheritance of individual trees (Bella, 1971; Hatch et al., 1975; Tomé and Burkhart, 1989; Barclay and Layton, 1990; Cole and Lorimer, 1994; Wimberly and Bare, 1996). However, this approach has been criticized. Diameter is related to the age and past competition history of the tree (Prévosto and Curt, 2004), rather than to actual social position. Growth rate is naturally related to tree size (Assmann, 1970) and its inclusion in the models could introduce ambiguity in the expression of the effect of competitive stress (Brand and Magnussen, 1988; Larocque, 2002). Ottorini (1991) mentioned that the close relationship between competition indices and tree size hampers the predictive ability of models that contain both variables. Lorimer (1983) pointed out that initial tree size can predict future growth effectively only when stand conditions do not change significantly, that is, in the absence of any condition or event that modifies stand density. Successful attempts to predict individual tree growth consisted in developing regression equations with both initial tree size (in terms of dbh or tree basal area) and a competition index as predictors (Tomé and

Burkhart, 1989; Barclay and Layton, 1990; Wykoff et al., 1990; Winsauer and Mattson, 1992; Cole and Lorimer, 1994; Wimberly and Bare, 1996; Moravie et al., 1999; Rautiainen, 1999). Even so, in the referenced studies the contribution of competition indices to the strength of the relationships was generally marginal.

Here, competition indices which do not incorporate additional information about tree status added little if any significance to a size-only null BAI model (e.g., Daniels' CI). An individual's ability to intercept light and to shade other competitors depend on its crown area (Hatch et al., 1975; Doyle, 1983; Holmes and Reed, 1991). In S.Maria, where belowground resources are not considered a limiting factor, including crown area in the CI significantly improved BAI models. This is consistent with expectations of competition for light being the predominant driver of tree growth after canopy closure; the asymmetric nature of this process is reflected in the good predictive power of crown areas on individual growth (i.e., CCS index). The self-thinning process, which has just began in this area, is thus considered to be promoted mainly by aboveground interference. This approach is consistent with the findings of Hix and Lorimer (1990), Ottorini (1991), Biging and Dobbertin (1992), Cole and Lorimer (1994) and Vettenranta (1999) that observed the inclusion of crown variables to improve the performance of their models. Lorimer (1983) and Biging and Dobbertin (1992) found that inclusion of crown class ratings for competitors refined competition estimation. Crown dimension is a result of past competition as well as an indicator of the current growth potential (Iwasa et al., 1984). According to Cole and Lorimer (1994), the use of crown variables increases the degree of accuracy of models when long-term predictions are made, as the limits of aerial space occupancy are more realistically defined.

On the other hand, the best overall prediction is provided in Morgex by a height-ratio based competition index (P.K.), capable of accounting for negative as well as positive outcome of competition and enhancing differences between suppressed and dominant/codominant individuals. Higher heterogeneity between trees may result in the pre-emption of resources (light) by taller individuals (D'Amato and Puettmann, 2004). Taking into consideration these results, we suggest the use in models of CIs bearing additional information relevant to competitive dynamics, i.e., crown area and height/dominance ratios in uniform and heterogeneous stands respectively.

The inclusion of spatial information (distance-dependent indices) improved model performance to a variable extent, unless tree distances were given too much weight ($R.K._2$), since the local component of competition was already accounted for by the competitor selection rules. In the most fertile site, a 10m-radius selection performed consistently better than selection based upon shorter distances. Miina and Pukkala (2000) found that pine competitors nearer than 6 m to the focus tree were included in an optimal competition index; Pukkala (1987) observed a higher survival probability for Scots pine seedlings 4 to 5 m far from overstory trees.

On the opposite, enlargement of competitive influence zone did not bring significant improvements in Morgex. Here, microsite fertility plays a major role, forcing trees to establish in small clumps with high size heterogeneity, and therefore increasing the importance of small-scale dominance-suppression relationships over interactions played on longer distances.

In general, the results and comparisons on the different competition indices have been quite variable. The performance of a particular index may vary with species, stage of stand development and cultural practices. No index has been shown to be universally superior (Huhn and Langner, 1999). Burton (1993) underlines that the most important limitation of any competition index is that it is static; it is a representation of the state of a dynamic system at one point in time, without any explicit considerations of the many sources of variation within a stand and from year to year. Instantaneous assessments cannot unequivocally determine the importance of interference, since system dynamics cannot be represented by one-time measurements (Burton, 1993). An additional limitation of the competition indices is the use of an arbitrarily chosen number of years to evaluate the effect of competition on tree growth (Peterson and Squiers, 1995). De Luis et al. (1998) evaluated 5 years to be the minimum time span to obtain reliable assessments of competitive influence in a 20-year old pine plantation, but variability of natural stands may require integration of much longer growth sequences for exogenous variability to be smoothed out.

The strength of the relationship between growth and neighborhood competition has usually been assessed by correlation analysis through the values of R^2 (Weiner, 1982, 1984; Raventos and Silva, 1995). However, the response variable (growth of subject tree) also affects, and has affected, the competitive neighborhood that is used as a regressor (Firbank and Watkinson, 1987; Peterson and Squiers, 1995), violating correlation and regression assumptions of independence. Furthermore, due to this fact in neighborhood models part of the variability in the results can be explained due to chance alone (De Luis et al., 1998).

Further work to confirm hypothesized dynamics will have to follow preliminary refinement of statistical tools used to infer competitive influence in order to overcome the mentioned limitations. Should quantitative accuracy of growth predictions be prioritized, all stages of the modeling process will have to be developed. This will involve both running model calibration on initial (rather than end-of-period) tree data, and providing ancillary growth data to perform reliable model validation (Reynolds, 1984; Mayer and Butler, 1993; Soares et al., 1995; Loehle, 1997; Huang et al., 2003). The comparison of model estimates with independent data from permanent plots is important especially when empirical forest models are used for estimating long-term growth trends, with or without anthropogenic influences, as decision support tools in forest management (Vanclay and Skovsgaard, 1997; Pretzsch and Dursky, 2001).

Conclusion

The analytic tools presented in this paper proved useful for the identification and investigation of stand dynamics on both a stand- and a tree-scale. We considered intertree competition as the main driver of stand development in eight study areas representative of the main Scots pine cover types in the northwestern Alps.

A first stand-scale competition assessment showed how competition intensity is related to stand developmental stage, tree density and past disturbance events. Discrepancies between competition-related mortality rates and observed frequencies of coarse woody debris allowed us to detect stands where exogenous disturbance processes had been or still were in progress.

The temporal development of competitive relationship was assessed by means of spatial statistics. Point pattern analysis helped in detecting the range of competitive interactions, which were confirmed to produce increasingly regular or over-dispersed patterns in individuals the main species. Past disturbances explained the occurrence of clumped tree patterns in other mature stands. Bivariate patterns evidenced ongoing successional dynamics; the differences in the realized niche of early-seral, mid-seral and tolerant regenerating colonizers were detected and imputed to stand history and past disturbance impact. Initial recruitment of pine stands was modeled after the age/size autocorrelation patterns observed in the study plots (secondary invasion, large gap-phase, small-scale establishment).

The effect of competition on stand-scale survival and size partitioning was conceptually modeled; the hypothesized development was confirmed by size hierarchies observed in the field.

Analysis at the tree scale allowed to disentangle the components of competitive dynamics. The importance of competition, as related to other regulatory factors, was found to increase consistently with relative density. Competition intensity, conversely, was found to express local interactions between trees, therefore it was not always proportional to competition importance.

The effect of competition on tree growth was assessed by means of individual competition indices used for the prediction of basal area increment. When incorporated into CI formulations, crown size and tree height were the most informative variables for diameter growth predictions, respectively in an homogeneous and spatially heterogeneous stand. Field evidence confirmed the prevailing role of competition for light in determining self-thinning. The performance of selected competition indices improved with increasing influence radius (up to 10m in a homogeneous stand) and growth period analyzed.

Land use history and site quality have been found to play a major role in determining intensity, importance and mode of current competition dynamics. Discrepancies in growth and mortality response of trees to neighbor competition were imputed to differences in size fertility, stand age structure and environmental resource type, with competition acting as a mediator between resource availability (input) and individual tree plastic response (output).

Along with many researchers, we have faced the difficulty of representing competition processes in forest dynamic models, and finding an adequate balance between simplicity, allowing easy interpretation, and complexity giving more realistic results. Our study shows that a stand-level analysis of competition, size asymmetry and tree spatial structure should also be used to support model predictions. Since changes in spatial pattern, mortality trends, spatial autocorrelation and size distribution are irrevocably linked (Miller and Weiner, 1989; Hara and Wyszomirski, 1994; Kenkel et al., 1997), their simultaneous analysis resulted in a much more complete view of stand dynamics than would be obtained from a series of independent analyses. The integration of multiscalar methods can help to explain the functional links between the analyzed processes and detect inconsistencies which may reveal local deviations from modeled trends.

Mathematical representations of competitive interactions at the individual level improved growth forecasts well, albeit sometimes a little. The obtained information was used to devise a basal area growth model for Scots pine, which was calibrated separately or two study areas differing in historical development and current structure. Furthermore, the information enclosed in stand- and tree-scale competition indices can be used to evaluate the role played by competition in health-related issues, such as the recent dieback wave taking place in inner-alpine Scots pine stands (Rigling et al., 1999).

The study areas detailed herein mark the establishment of a network of permanent monitoring areas, that will allow direct evaluation of stand development by repeated sampling through time (Curtis, 1983; Vanclay, 1992; Motta et al., 2002). Since only one measurement has been carried out so far, stand dynamics had to be inferred from "snapshots" of structure and processes taken at different developmental stages. Growth measurements on seedlings, saplings, and mature trees on permanent plots, in relation to measurements of local resources, provided the best source of data for characterizing the response of species to resource variation, which included the feedback of neighboring trees on resource availability. In the absence of long-term data, the use of tree rings to measure past growth along resource gradients provided a means for quantifying species-specific growth-responses (Pacala et al., 1994). Extending long-term ecological studies like the one detailed herein will provide adequate data for validating model results and capturing slow phenomena, rare events, as well as subtle and complex processes (Pickett, 1991).

Chapter IV: Testing suitability and calibration power of an individual-based, spatially independent stand growth model[10]

Introduction

Archived forest data offer the possibility of obtaining an overview of the trends and patterns that are occurring over space and time. By linking such trends and patterns to other factors and features, including human intervention, it is possible to interpret and understand causative relationships between forest, environmental and intervention variables and factors. Such interpretation and understanding has generally been sought by building mathematical and statistical models which describe or explain the trends, patterns and relationships in the data.

The Fort Bragg military reservation in North Carolina [Figure 39] includes over 29,000 hectares of longleaf pine (*Pinus palustris* Mill.) forest (Blythe et al., 2001), one of the largest remaining contiguous tracts of the type. It is also home to one of the largest populations of the endangered red-cockaded woodpecker (*Picoides borealis*). Fort Bragg and adjacent properties form a primary core population in the Sandhills Recovery Unit (U.S. Fish and Wildlife Service, 2003). As a result, the red-cockaded woodpecker (hereafter, RCW) population at Fort Bragg is intensively monitored and managed. To manage the RCW effectively, it is necessary to manage its habitat.

Management goals that include maintenance of stand composition and structure are accomplished through a combination of silvicultural manipulations and

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[10] Based upon Shaw. J.D., Vacchiano G., DeRose R.J, Brough A., Kusback A., Long J.N. (2006), *Local Calibration of the Forest Vegetation Simulator (FVS) Using Custom Inventory Data*, proceedings of SAF National meeting, Pittsburgh, October 25-29, 2006, 10 pp.

prescribed fire. Inventory data are required to assess the suitability of forest conditions according to the RCW recovery guidelines (U.S. Fish and Wildlife Service, 2003). An installation-wide forest inventory was conducted on Fort Bragg in the early 1990s. The data provided by this inventory were to be used for assessment of the quality and quantity of suitable RCW habitat, as well as for identification of acreage in need of restoration treatments. In the twofold interest of planning for future growth of the forest and development of military facilities, the inventory contract required 10-year growth projections, at the stand level, for the entire installation. However, growth projections provided by the contractor appeared to be unrealistically high when compared with the stocking levels known to be attainable on the dry, sandy soils characteristic of Fort Bragg and much of the Carolina Sandhills. In subsequent evaluations, other growth models showed similar tendencies. When planning for a new inventory started in 2000, no suitable growth model had yet been found.

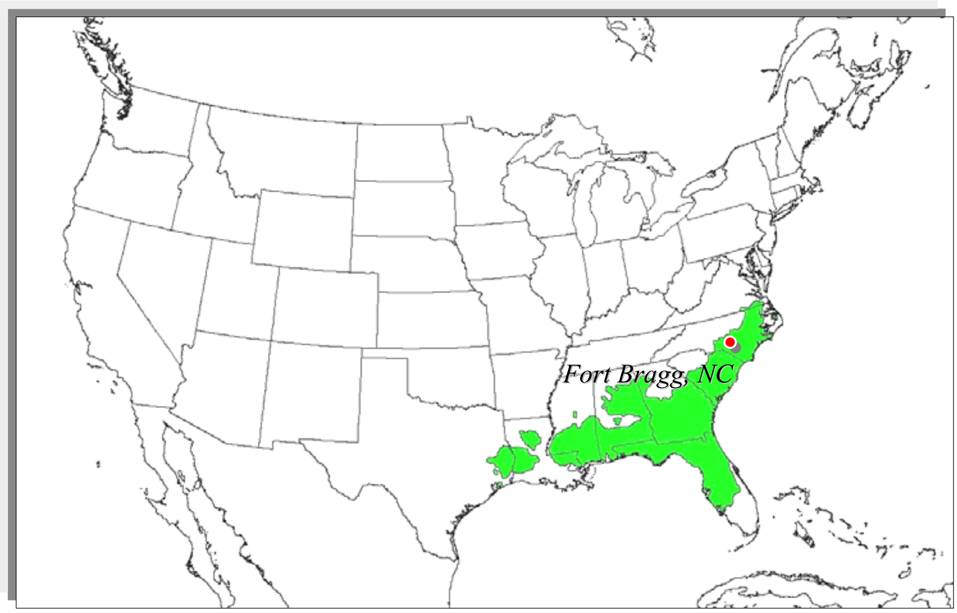


Figure 39 –Distribution of Pinus palustris *Mill. in USA and localization of the study area (modified from Prasad and Iverson, 2003).*

The Forest Vegetation Simulator (FVS) is a distance-independent, individual-tree empirical growth model that is the standard stand projection tool used by the USDA Forest Service (Johnson, 1997; Dixon, 2006). During the 1990s, the Forest Service made significant improvements to FVS, including development of a new variant of the model calibrated with data from the Southern states (Donnelly et al., 2001). Preliminary testing of the Southern variant indicated that it, too, would overestimate growth on Fort Bragg. However, the capabilities offered by the FVS framework – such as the ability to simulate silvicultural manipulations and linkage to stand visualization tools such as the Stand Visualization System (McGaughey, 2002) – suggested that FVS could provide a useful framework under which a suitable growth model for Fort Bragg could be developed.

As a result, we proposed modification of the 2000 Fort Bragg inventory to include variables needed for evaluation (*sensu* Vanclay and Skovsgaard, 1997) and, if necessary, re-calibration of the FVS model, both as a whole and in its components. Each of the component submodel consists of one or more growth equations, depending on program logic. This allows submodels to be developed concurrently in the variant development process.

Our objective is to develop a "Fort Bragg variant" of FVS, emulating the workflow process used by the USDA Forest Service, Forest Management Service Center during the development of the Southern and other FVS variants. In this paper we describe the inventory design, data collection, and model development that have been accomplished to date. Although designed specifically for Fort Bragg, the process is applicable to many situations where local evaluation and fine-tuning of FVS is needed.

Synopsis of forest simulation models

Simulation can be defined as the imitation of the operation of real-world systems or processes over time. It is the process of experimenting with a model of the system under study, measuring a model of the system rather than the system itself (Garcia, 1974). Therefore, models provide a means of formalizing a set of hypotheses that link pattern and process.

Foresters have been using various kinds of growth model for at least two hundred years. Yield tables for pure stands are the oldest models in forestry science and forest management (e.g., Hartig, 1795). Notable milestones in the development of modern growth models include the compilation of arithmetic growth formulae (e.g., Schneider, 1853, cited in Vanclay, 2003), alignment charts (Reineke, 1927), biologically-based growth formulae (Schumacher, 1939; von Bertalanffy, 1941), statistically-derived growth equations (McKinney and Chaiken, 1939), matrix models (Leslie, 1945; Usher, 1966), compatible growth and yield equations (Buckman, 1962; Clutter, 1963), computer-based individual tree models (Newnham, 1964), gap or successional models (Botkin et al., 1972). Discussions of the history of tree and forest ecosystem modeling can be found in Shugart et al. (1992), Botkin (1993), Botkin and Schenk (1996), Landsberg (2003), and Monserud (2003); the state-of-the-art has been reported in several conferences (e.g., Fries, 1974; Dudek and Ek, 1980; Mason and Muetzelfeldt, 1986; Ek et al., 1988; Burkhart et al., 1989; Wan Razali et al., 1989; Dixon et al., 1990; Wensel and Biging, 1990; Vanclay et al., 1993; Foli et al., 1997; Amaro and Tomé, 1999; LeMay and Marshall, 2001; Rennolls, 2001; Hasenauer and Makela, 2004), and much of the accumulated knowledge is summarized in some key texts (Vanclay, 1994; Alder, 1995; von Gadow and Hui, 1998; Amaro et al., 2003; Hasenauer, 2005).

This diversity in application and development has induced an extraordinary array of different models in forest science and management. The University of Kassel maintains an internet-based Register of Ecological Models (Benz and Knorrenschild, 1997) with references to over 680 models (as in December, 2006); the Forest Model Archive (FMA) is a repository of forest models developed in all parts of the world over many decades of continuing research (Rennolls et al., 2001). Dale et al. (1985) noted that there were several hundred computer models that project changes in forest stands by simulating the growth, and possibly dynamics, of individual trees.

To get an overview of the state-of-the-art in the field of modeling forest dynamics, a classification of the existing models forms a helpful tool. In the literature, however, several, generally contradicting classification schemes were found (Munro, 1974; Shugart, 1984; Shugart et al., 1988; Vanclay, 1994; Houllier, 1995; Pretzsch, 1999; Franc et al., 2000; Porté and Bartelink, 2002). Two broad categories can first be distinguished based on the purpose the model is built for, i.e., "descriptive" or "explanatory" forest dynamics models. The first group refers to empirical models, containing relationships statistically fitted on data (see later in this chapter). The second group aims at mechanistic or "process-based" models explaining growth using the biological, physical and chemicals processes involved (Shugart et al., 1992; Mohren and Burkhart, 1994; Pacala et al., 1996; Chave, 1999; Bartelink, 2000; Franc et al., 2000; Landsberg, 2003; Makela et al., 2003).

Empirical models tend to use time and space in a simple and direct way. Time is used as an explanatory variable in a growth curve such as the logistic equation, so that the value of the variable under consideration (e.g., height) at any time can be known just by appealing directly to the function. Some measure of spacing is usually used to assess competitive interactions among objects, either directly, as a collection of tree distances, or indirectly, e.g., as a local basal area. Empirical methods of modeling the growth of trees and stands describe the change in number and dimension of trees or stands with time-dependent functions based on past observations of growth under similar conditions (e.g., Stage, 1973). The major drawback of this approach, where tree or stand growth is estimated using descriptive relationships, is the restricted applicability of the models due to the limited validity of the empirical relationships (Porté and

Bartelink, 2002). On the other hand, process models are devoted to the tracking of individual processes that drive growth (Bugmann, 2001). Trees grow larger because they accumulate carbohydrates in a time-controlled process that depends on photosynthesis, not merely because they age. Similarly, trees do not attenuate growth because they happen to be a certain distance away from one another, or because the local basal area is too high. Instead, they attenuate growth because they receive less of the available resources, be that light energy, nutrients, or moisture. These resources are intercepted by other "competing" plants (Robinson and Ek, 2000)

A further distinction for all models is whether they are *static*, and describe how a state of the system will be at a certain time (a commonly used state variable is standing volume), or *dynamic*, and describe how the state of the system will change across a fixed time span, e.g., using basal area increment as the predicted variable (Garcia, 1994). Porté and Bartelink (2002) proposed a revised classification of forest models, integrating the previous proposals. The authors made a first distinction with respect to the **spatial level** at which the forest is modeled, i.e., stand or global models and individual-based models or individual growth models, corresponding to the smallest unit identified (i.e. a branch, a tree) in the model. The second criterion was **spatial dependence** (whether these units have specific spatial locations or not); and the third criterion described whether or not forest **heterogeneity** is taken into account [Figure 40].

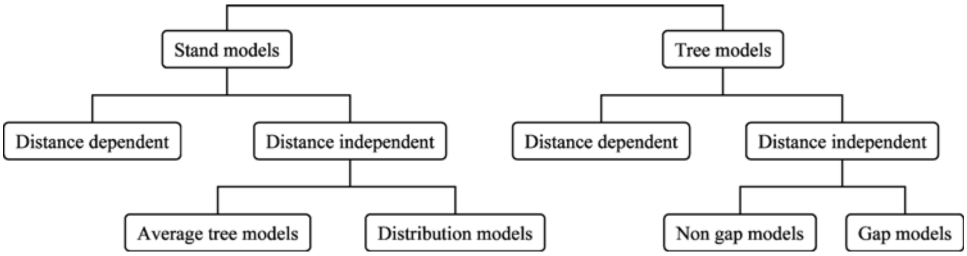


Figure 40 – Classes of forest simulation models (Porté and Bartelink, 2002).

Apart from the difference between empirical and mechanistic models, a distinction can be made with respect to spatial resolution, i.e. between global and individual approaches. In the stand-level approach, no individual trees are described and the canopy is represented by horizontally homogeneous leaf layers. Most stand-level models are empirical models, such as the yield tables. Stand-level models are by their very nature unable to represent different planting patterns in mixtures, or to take account of spatially non-systematic thinning measures. Neither can they take crown dynamics into account.

In contrast, individual based models (IBM) simulate the performance and fate of individual organisms in ecological systems (Huston et al., 1988; DeAngelis and Gross, 1992; Judson, 1994). The individual-based approach holds that the properties of a system are derived from the properties of its parts and the relations between them (Lomnicki, 1988). the performance of each individual is simulated and a set of individuals is taken to represent the dynamics of the system (Metz and Diekmann, 1986). Characteristic of these models, also defined single-tree models (Vanclay, 1994), is that these models describe and keep track of each individual tree in the stand: the overall dynamics of the forest depends on the combined dynamics of the set of trees simulated. The first individual-tree model was developed by Newnham (1964) for pure Douglas fir stands. In the mid- ‘70s, Ek and Monserud transferred the design principles of individual-tree growth models from pure stands to uneven-aged pure and mixed stands (Ek and Monserud, 1974; Monserud, 1975). Forest IBMs have been reviewed to some extent by Ford and Sorrensen (1992), Shugart et al. (1992), Liu and Ashton (1995), Grimm et al., (1999), Franc et al. (2000), DeAngelis and Mooij (2005).

Individual-based models were successful for several reasons (Judson, 1994). First, information on the biology and life history of individuals is often available, facilitating model parameterization. Second, the breadth of information that is generated by individual-based models is sufficient to address a wide range of problems from individuals to ecosystems (Busing and Mailly, 2004). All individual-based simulation models of forests share an emphasis on capturing the performance of individual trees, but they vary greatly in their degree of spatial complexity (Bugmann, 2001). In most cases the main component of IBMs is a system of different equations controlling the growth behavior of individual trees in relation to spatial stand or plot structure (Pretzsch et al., 2002).

Gap-models can be classified as a special category of tree-level modeling, as they define and keep track of individual trees competing and growing in a restricted area, the gap (Botkin et al., 1972; Shugart, 1984). Gap models and tree-level models are more flexible than stand-level models, but generally rely heavily on descriptive relationships. Models that include biological processes and are suitable to support taking decisions about forest management would constitute a great advantage, but unfortunately are still scarce (Mohren et al., 1991). On the other hand, though mechanistic approaches do relate growth to growing conditions, these are in general too theoretical or require too many data to be of much value for forest managers.

In complex systems like mixed or multi-layered forests, tree-level models are considered necessary to account for competition effects: the differing characteristics of the species and the spatial distribution of the trees have a different and in most cases a much stronger impact on stand development than is the case in monospecific forest stands. The descriptions of tree-to-tree interactions are thus necessary to provide reliable estimates of stand development. Due to the required spatial detail, tree models, in many cases, seem to offer the best opportunities to support silvicultural research and forest management decision taking. The simulation of inter-tree competition allows in principle a detailed prediction of stand structure, growth and yield, and biodiversity and is hence a promising tool (Porté and Bartelink, 2002).

The spatial location of trees constitutes the second discriminating criterion in our classification, separating distance-dependent tree models (DDTM), where the tree location is known, from distance independent tree models (DITM) that consider the forest as one unit, without any within-spatial organization. In DDTMs, the stand is described as a mosaic of forest patches. Each patch is characterized by its location in the stand and has its own dynamics, which is interacting with the dynamics of the neighbor patches. With respect to tree models, both distance-dependent and distance-independent tree models have been applied for growth and yield research. Tree level outputs integrated at the stand level present a quality of prediction not as good as for stand level models but they are still consistent with short- and long-term observations (Shugart et al., 1980; Waldrop et al., 1986; van Daalen and Shugart, 1989; Pacala et al., 1996; Moravie et al., 1997).

Porté and Bartelink (2002) further distinguished DDTMs between those that do and those that do not describe the heterogeneity of the stand: the stand can be described either as the sum of N average (identical) trees (no heterogeneity) or is divided into i size classes, each class consisting of N_i average trees. This third criterion resulted in two groups of models, being "average tree models" and "distribution models". Average tree models describe the stand using stand level variables such as the number of stems, average tree dimensions, stand dimensions (volume, basal area, etc.). Distribution models also model the average and total dimensions of the stand per tree species, but they differ from the previous group by partly integrating the natural variability among the trees in a stand. Each modeled characteristic of the stand is then described by a distribution function, either continuous or discrete (dimension classes) hence implicitly defining different size classes.

Finally, irrespective of its detail, a model may be deterministic or stochastic. A deterministic growth model gives an estimate of the expected growth of a forest stand. Given the same initial conditions, a deterministic model will always predict the same result. However, because of natural variation in the environment, real forest stands may not grow exactly the same amount each year, but may grow more or less than the expected amount. A stochastic model attempts to illustrate this natural variation by providing different predictions, each with a specific probability of occurrence. Any one of these estimates may correspond exactly to the growth under some circumstances, but may differ from the expected growth. A single estimate from a stochastic model is of little use, as a whole series of estimates is necessary to provide useful information of the variability of predictions (Vanclay, 1994).

The modeling process

Common usage of the term "growth model" generally refers to a system of equations which can predict the growth and yield of a forest stand under a wide variety of conditions. Thus a growth model may comprise a series of mathematical equations, the numerical values embedded in those equations, the logic necessary to link these equations in a meaningful way, and the computer code required to implement the model on a computer (Vanclay, 1994).

According to Bruce (1990), there are three distinct types of model functions: driving functions, housekeeping functions, and structural functions. Driving functions are those functions which actually characterize the dynamic nature of stand and/or tree development. Examples are height growth, diameter growth, or basal area growth. The primary driver is that function which comes first in the progression of forecasts. Other drivers will be considered secondary. Primary drivers used in single-tree models are usually identified as diameter (or basal area) increment, mortality and recruitment [Figure 41]. Housekeeping functions are those functions which may vary between simulators and even between species within a simulator but which do not directly impact the dynamic nature of the simulator itself. Examples are volume equations or some species-dependent indices of stand density such as crown competition factor (Krajicek et al., 1961). Structural functions are common functions invariant across species and simulator. Examples are calculations for stand basal area or stems per acre (Ritchie, 1999).

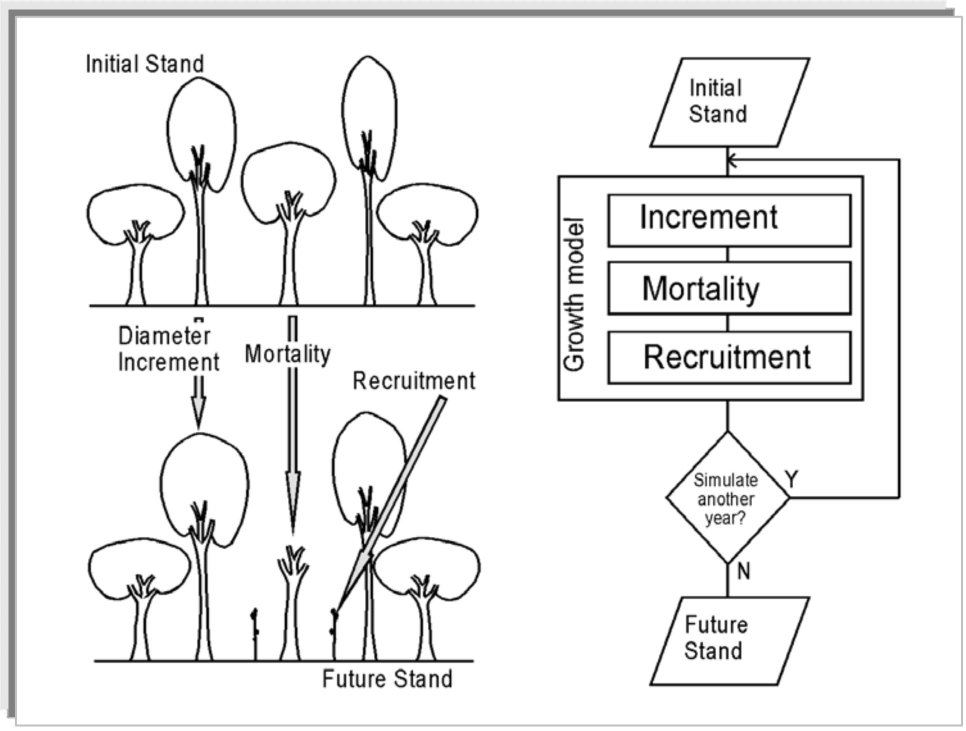


Figure 41 - Components of forest growth and the analogous representation in a stand growth model (from Vanclay, 1994).

The process, which ends with the formulation of an ecological model (including forest G&Y models), has been thoroughly examined by Vanclay (1994) and Guisan and Zimmermann (2000) [Figure 42]. After the preliminary delineation of the conceptual model (i.e., underlying ecological concept or process to be represented), the course model building must go through three main steps:

1. *Statistical formulation*, that implies the choice of a suited algorithm for predicting a particular type of response variable and estimating the model coefficients, and an optimal statistical approach with regard to the modeling context.

2. *Calibration.* This step results in the adjustment of the mathematical model that was selected for the specific data set at hand. Rykiel (1996) defined calibration as “the estimation and adjustment of model parameters and constants to improve the agreement between model output and a data set”. Guisan and Zimmermann (2000) included in this step both the selection of explanatory variables, which must be reduced to a reasonable number (Harrell et al., 1996), and the estimation of their coefficients. The fit of the model is then characterized by a measure of variance or deviance reduction (Weisberg, 1980), allowing to compare models that include different combinations of variables and interaction terms. Generally, the model for which the deviance reduction is maximal is considered as the best, and further used for prediction purposes (Reynolds et al., 1988).

3. *Evaluation* (Soares et al., 1995; Rykiel., 1996; Vanclay and Skovsgaard, 1997), a complex process that should try to reveal any errors and deficiencies in the model by (i) assessing the model and its components in terms of logic structure and from theoretical and biological or ecological views (Loehle, 1983), (ii) determining the statistical properties of the model in relation to data, (iii) characterizing model accuracy and precision (Gregoire and Reynolds, 1988; Reynolds et al., 1988), the magnitude of bias and error structure (Reynolds, 1984); (iv) conducting uncertainty and sensitivity analysis of the model components (Rabitz, 1989; Mowrer, 1991; Saltelli et al., 2004). Two main approaches exist for evaluating the predictive power of a model, i.e., using a single data set to calibrate the model or using two independent data sets, one for calibrating and another for evaluating the model (often called the training and evaluation data sets (Guisan and Zimmermann, 2000). *Re-calibration* refers to the search for adjustments to improve model predictions for a specific locality. It relates to model evaluation, because if benchmark tests reveal deficiencies in a model,

the question is if the same data may be used to re-calibrate the model so that predictions are improved for that locality, and if so, how (Vanclay, 1994).

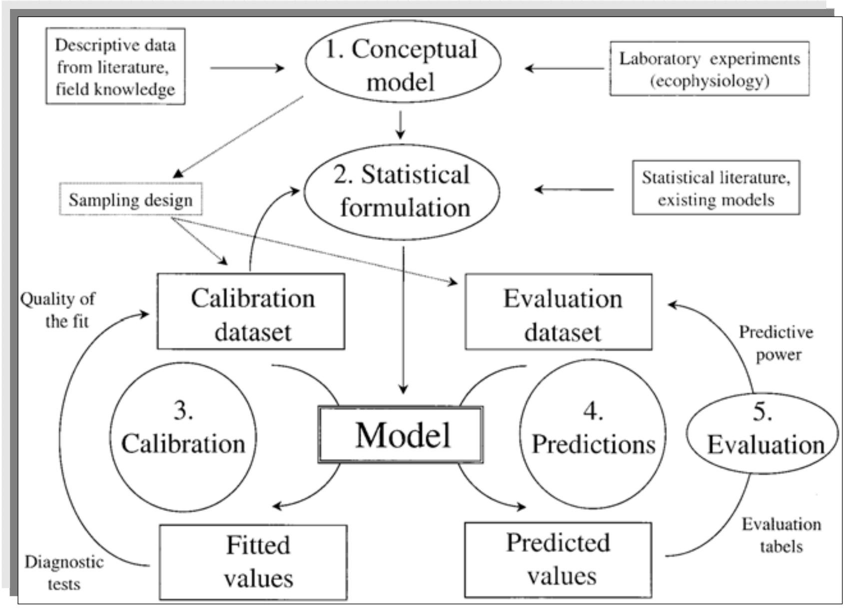


Figure 42 - Overview of the steps required by the model building process, when two data sets – one for fitting and one for evaluating the model – are available (from Guisan and Zimmermann, 2000).

Data requirements

Ultimately, all models rely on data to estimate coefficients, to calibrate and evaluate models, and to initialize simulations. All too often, the modeling approach is dictated by limitations of the data. Forest growth models are usually calibrated on two types of data sources:

- long-term field experiments, which provide long time series, with detailed information on tree and stand growth. These data reveal mathematical relationships of growth at individual-tree and stand level and permit model development, parameterization and validation.

- Snapshot inventory data, that will impart less detailed information, but will give rather more general information on growth on larger areas.

Continuous forest inventories based on permanent sample-plot design are well suited for the parameterization and evaluation of models, but the two data sources can complement each other (Curtis and Hyink, 1984; Pretzsch et al., 2002). Data requirements of many modeling approaches are similar and allow a set of minimum procedures to be established. Vanclay (1994) discussed the procedures and requirements for development of data suitable to growth and yield models, asserting that only permanent sample plots (PSP) allow satisfactory statistical comparisons within and between plots to check the adequacy of models, and provide reliable and consistent data on mortality, crown dynamics and stand level variables (McQuillan, 1984). Permanent plots should cover extremes of site and treatment; periodic reviews of data collection policy are necessary; quality of data collected is of extreme importance; and documentation should be complete, consistent and accurate. Adlard (1990) emphasized three factors: relevance, reliability and relationships. Curtis (1983) provided a comprehensive reference manual for PSP establishment and maintenance in temperate regions.

All individual-tree simulators require a list of sampled trees to make forecasts of stand development over time. Some are capable of generating a list from some stand-level parameters. The treelist variables usually include diameter at breast height (DBH), height, crown ratio, and expansion factor. Trees may be sampled on fixed- or variable-radius plots, or even on a combination of the two for most simulators. Such data should not only sample a range of stand and tree conditions, but must also include remeasurements to enable detection of change, and must include a sufficient time period to average any climatic variations, and to ensure that growth patterns are not obscured by measurement error. Forest models usually describe phenomena using a discrete time step varying from 1 to 10 years, so the measurement lag should follow accordingly to the model planned for use. The simulator will forecast changes in diameter, height and usually live crown ratio for each growth interval, as well as mortality. The tree list data are updated and represent conditions forecast for some future period.

The Forest Vegetation Simulator (FVS)

The Forest Vegetation Simulator (Wykoff et al., 1982; Dixon, 2006) is used extensively throughout the United States in a variety of ways to support contemporary forest management decision making. Originally developed as a model to predict stand dynamics in the mixed forests of the inland mountains of northern Idaho and western Montana (Prognosis Model for Stand Development [Stage, 1973]), FVS was chosen as a common modeling platform in the United States Department of Agriculture, Forest Service in 1980 (Crookston and Dixon, 2005). Twenty geographically-specific versions of FVS, called variants, have since been calibrated on local inventory data and currently cover most forested areas of the conterminous 48 states and southeast Alaska [Figure 43]. The methods used to predict growth and mortality are different among them. The form of driving functions (what variables are included) and the individual species designators may vary between variants and within variants between species. This information is provided in the documentation file associated with each variant.

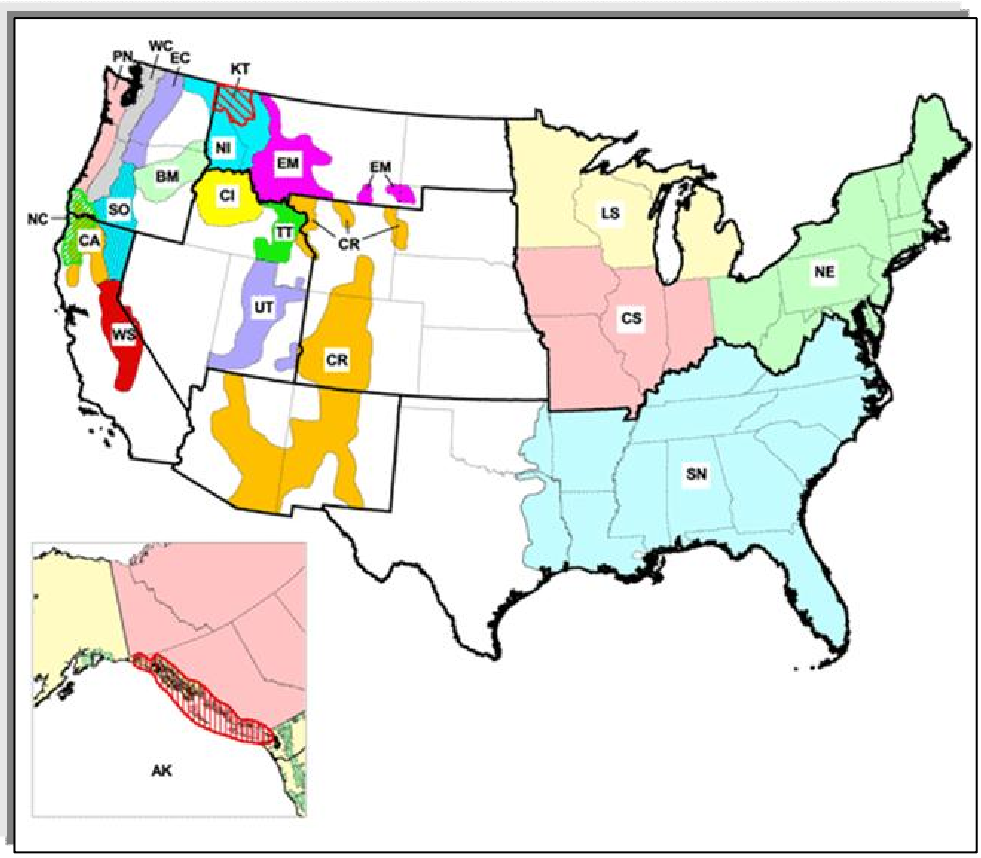


Figure 43 – Regional variants of FVS (from USDA Forest Service, 2006).

The model supports specification of management rules in the input, and includes numerous extensions developed which allow users to integrate such factors as disturbance agents (e.g., Courter et al., 2002), fire behavior and effects (Reinhardt and Crookston, 2003), physiological determinants of tree growth (Milner et al., 2003) regeneration establishment and shrub cover (Moeur, 1985) into growth and mortality forecasts. Post-processors and other programs can be used for FVS output and for further reporting, display, or analysis (Van Dyck, 2005). More general documentation on execution may be found in Wykoff et al. (1982) and Wykoff (1986). Wykoff et al. (1990)

documented execution of the Prognosis model core, version 6 for all existing variants. Refinement of model mechanics, development and testing of geographical variants, implementation of new extensions and applications are continuously underway, and are detailed by periodic conferences (Teck et al., 1997; Crookston and Havis, 2002).

Model structure

FVS belongs in the distance-independent, individual-tree class of models. Stands are the basic unit of management, and projections are dependent on interactions among trees within stands. The key state variables for each tree are density, species, diameter, height, crown ratio, diameter growth, and height growth. Key variables for each sample point, or plot, include slope, aspect, elevation, density, and a measure of site potential. The same information is available at the stand level. Time steps, or growth cycles, are generally between 5 and 10 years long, and the total projection is between a few years and several hundred years.

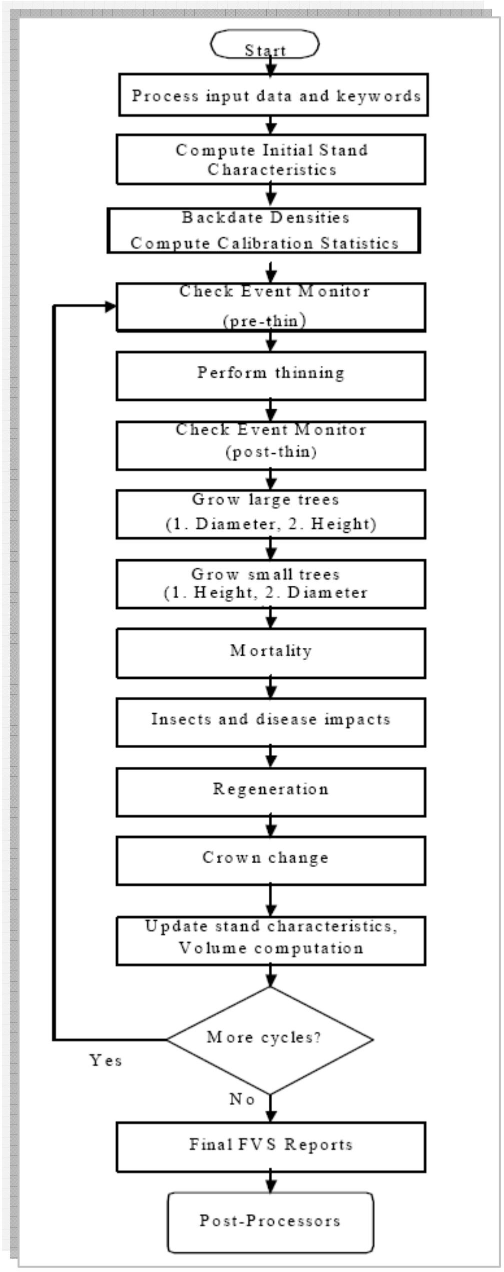
Two input files are generally used when running FVS. The first, a keyword record file, is required to enter stand level parameters, describe management treatments, control the printing of output, compute custom variables, and adjust model estimates. Keywords come with associated data providing information necessary and specific to the keyword action. For a list of available keyword-based operations, see Van Dyck (2006). The second input is the a tree data file, that is composed of records containing tree level information. Tree list variables include:

- plot identifier (integer)
- tree count (number of trees represented by the sample tree)
- species (two letter code)
- DBH

- DBH increment; period of this increment should correspond to the growth increment of the variant
- height
- height to topkill
- height increment; period of this increment should correspond to the growth increment of the variant
- crown ratio (integer code from 1-9)
- damage code(s)

Species and diameter at breast height are required on each tree record; crown ratio, crown width and tree height may be filled in by the simulator. A projection begins by reading the inventory records (treelist file) and the keyword-based descriptions of site and selected management options (Crookston, 1990). Input tree records with missing heights or crown ratios have these dubbed in; the inventory is then compiled to produce tables that describe initial stand conditions. When this summary is complete, the first projection cycle begins [Figure 44].

Figure 44 – Phases of the FVS program execution. Each projection cycle starts checking if any custom variables need to be computed or management activities scheduled based on pre-thinning stand conditions. Next, any silvicultural actions that have been scheduled for the cycle are attempted. Then periodic diameter increment, periodic height increment, and periodic mortality rate are computed. These estimates are then adjusted for effects of insects and pathogens. Tree records resulting from regeneration within the cycle are created next, and change in crown ratios are computed for each tree record in the projection. FVS updates tree records and repeats the sequence for each cycle until the specified number of cycles is completed. Then, tree volumes are calculated, and output tables reports and post-processor files that summarize projected stand conditions are compiled (from Dixon, 2006).


Start
Process input data and keywords
Compute Initial Stand Characteristics
Backdate Densities
Compute Calibration Statistics
Check Event Monitor (pre-thin)
Perform thinning
Check Event Monitor (post-thin)
Grow large trees (1. Diameter, 2. Height)
Grow small trees (1. Height, 2. Diameter
Mortality
Insects and disease impacts
Regeneration
Crown change
Update stand characteristics, Volume computation
More cycles?
Yes
No
Final FVS Reports
Post-Processors

The Southern Variant: features and challenges

Development of the Southern Variant of FVS (SN) began in 1998. Initial testing began in late 1999 and early 2000. Initial testing release was in April 2000 (Donnelly et al., 2001). The variant was developed from Forest Inventory and Analysis (FIA) data, Forest Service Research data, and data from the Bureau of Indian Affairs. Its geographic coverage is from most of the Southeastern United States (U.S. Forest Service Region 8)[11]. Growth relationships for such a wide area are refined with the help of species-specific coefficient arrays for each model equation; diameter increment and standing volume computations also include location codes accounting for the Region, National Forest, and Ranger District where the stand is situated, and Ecological Unit Codes (Keys et al., 1995) at the Province level as a means of distinguishing between major geographic areas within the South (see Donnelly et al., 2001 for a list of species and sites included in the model).

Except for volume and diameter increment, all the submodels portray average growing conditions and allometric relationship throughout the Southern States. The Fort Bragg area belongs entirely in the Sandhills Ecological Unit (Code 232Bq), but preliminary screening of model predictions evidenced a systematic yield overprediction bias for Fort Bragg stands as related to other areas within the same Unit. Even if the model includes a self-calibration feature, allowing it to adjust diameter and height growth predictions based on field increment data (Crookston and Dixon, 2005) there are grounds to suspect that local variability is not adequately reflected using only the described devices. Developers of SN stated that “If further research and/or evidence shows that tree growth differences are distinguishable at finer scales, such results can be fit into the

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[11] 13 States including parts of Oklahoma and Texas, Louisiana, Alabama, Georgia, Florida, South Carolina, North Carolina, Arkansas, Missouri, Virginia, Kentucky and Tennessee.

growth relationships at subsequent time" (Donnelly et al., 2001). The same was stated with specific reference to the diameter growth submodel[12].

Last, model documentation reports that when a species is included in the input tree list but was not calibrated for this specific variant, it is mapped to an appropriate surrogate species for growth simulation (USDA Forest Service, 2004). Such a procedure can entail significant bias when imputing crown width from tree dbh and when computing site indices to be used in growth relationships. Details of this process are described in Donnelly et al. (2001).

Localization of SN to better fit Fort Bragg growing conditions and correct for yield prediction bias at the model and submodel scale has therefore represented the main challenge in the modelling effort. A major aid in this process was brought by the exhaustive documentation coming with the model variant, that allowed us to "debunk" the inner model mechanics and test the predictions of each re-calibrated submodel against actual field data from the repeated stand inventory. Appendix 1 shows comprehensive flowcharts that detail the whole modelling sequence, including submodel functioning and references to model coefficients. Information from the SN documentation (Donnelly et al., 2001) were integrated with general FVS manuals (Stage, 1973; Wykoff et al., 1982, 1986, 1991) and updated according to the periodic FVS bulletins issued by the USDA Forest Service and to the most recent version of the working Fortran SN program code (January, 2006).

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12 "The connections between our set of predictor variables and physiological processes that actually control tree growth are, at best, tenuous. Therefore, it is unreasonable to assume that growth responses in locations with substantially different environmental limitations will be the same. It is more likely that the shape of the response surface in these locations, relative to our set of predictor variables, will be different. When this is the case, the models should be refit" (Donnelly et al., 2001).

Methods

Inventory Design and Data Collection

Using documentation of the Southern Variant (Donnelly, 1997), we developed a list of measured and computed variables that would be necessary for fitting the submodels to Fort Bragg data. This list was used when writing specifications for the 2000 inventory contract. The Southern variant was developed using a variety of data sources and, as a result, considerable effort was required to bring the data into a common format (D. Donnelly, personal communication). By integrating the FVS-ready variables into the inventory design, we minimized the amount of effort required for data development [Figure 45]. Measured variables were separated into 3 groups that would be collected at different intensities: 1) ordinary variables were measured for every tally tree on every plot (dbh > 5 cm as determined using a 10 BAF prism count), 2) site tree variables were measured on one dominant or codominant pine on approximately every other plot, and 3) intensive variables were measured on every tree > 12.7 cm (5 inches) dbh on plots designated as intensive measurement plots (approximately 5% of all plots).

The forested area of Fort Bragg was delineated into stands, with a minimum polygon size of 2 ha, using digital orthophotography and GIS. This yielded 1,384 stands, ranging up to 243 hectares in size. Stands in firing ranges and ordinance impact areas could not be inventoried because of potential danger to crews and were assigned to surrogate stands that could be inventoried, based on airphoto analysis of composition and structure.

Plots were installed at an intensity of approximately 2.5 plot per hectare (1 plot acre^{-1}), depending on stand size. The number of plots per stand ranged from 5 to 83 for a total of 18,286 plots. Plots were assigned to one of 3 different types – ordinary, site, and intensive – which determined the number of variables to be measured and which trees were measured. For example, on ordinary plots, basic data – species, dbh, tree status, dominance class, etc. – were measured on all trees. On site plots (approximately ½ of plots), height, age, and other variables were collected on the dominant tree on the plot. On intensive plots, increment data and crown dimensions were measured on all trees > 12.7 cm dbh. Plot- and tree data were imported into a Microsoft Access database and screened for invalid values. A small number of tree records were deleted or modified because of questionable data in one or more fields. After screening the database, the additional variables needed for model development were calculated [Table IV.1]. A total of 140,131 trees was sampled for ordinary variables; of these, 6% were sampled as site trees and 2.5% were intensively measured. Table IV.2 reports the mean value and ranges for some of the sampling variables.

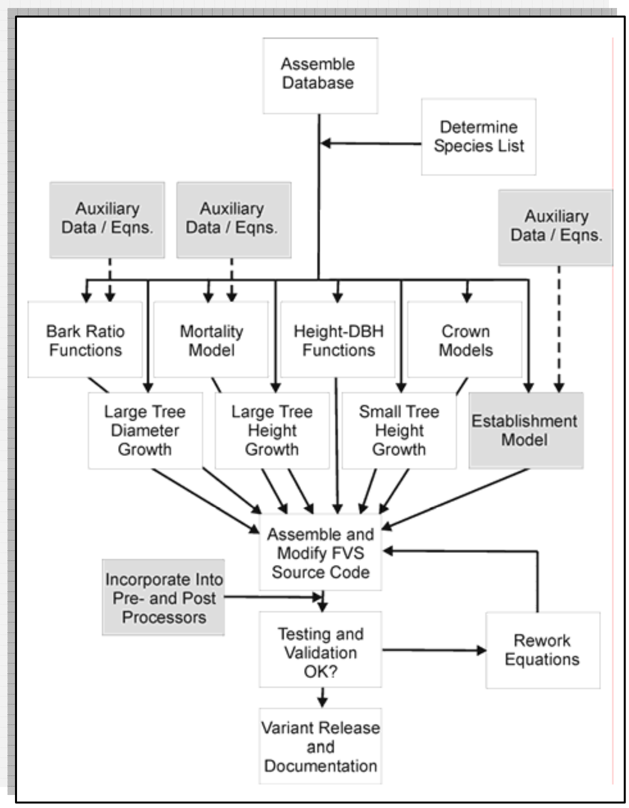

Figure 45 – Work process for development of a Forest Vegetation Simulator (FVS) variant (after Johnson et al., 1998). Shaded steps are not needed in development of the Fort Bragg Variant.

Table IV.1 – List of measured and computed variables included in Fort Bragg final database after the year 2000 inventory.

Tree variables	**Stand (plot) variables**
ID codes	ID codes
Inventory type	Inventory type
Species (FIA codes[13])	Inventory date
Dbh	Spatial location (UTM NAD_{83})
Rank (stand-wise dbh distribution)*	Trees per hectare[14] *
Point Basal Area Larger[15]*	Quadratic mean dbh*
Total Height	Basal area*
Crown width$_{1,2}$	Additive Stand Density Index*
Crown width mean*	Reineke's Stand Density Index*
Crown ratio estimate	$SDI_{sum}/SDI_{Reineke}$ ratio
Tree crown class estimate[16]	Relative SDI*
Height to crown base	Species-specific Site Index[17]
Live crown ratio	Species-specific asymptotic height[18]*
Radial increment	Point Basal Area*
5-year diameter increment	Slope %
Basal Area (outside bark)*	Slope (°)*
Age at breast height	Aspect (°)
Age*	Forest type code[19]
Relative height (Height H_{40}^{-1})*	EUC
Tree condition code[20]	H_{40}[21]*
Bark thickness	Age minimum, maximum*
Bark ratio*	Age mean, median*

* = computed variable (not measured).

Black = Phase 1 measurements (dbh > 5 cm)
Red = Phase 2 measurements (dbh > 5 cm)
Blue = Phase 3 measurements (dbh > 12.7 cm)

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[13] USDA Forest Service, 2005.
[14] Both including and not including regeneration plots (dbh <2.5 cm).
[15] Stage and Wykoff, 1998.
[16] Dominant, codominant, overtopped, intermediate.
[17] Calculated from the average dominant and codominant tree (base age 50).
[18] Back-calculated as a power function of SI.
[19] Determined as species with maximum share of SDI per stand.
[20] live and healthy, live, deformed, live/insect damage, live/diseased, live/physical damage, dead/recent, dead/old.
[21] Average height of the per-acre 40 largest diameter trees.

Species	**Sample size**	**Sample frequency**	**DBH [cm]**			**Height [m]**				**Age at breast height**			
			Mean	**St.dev.**	**Max**	**Mean**	**St.dev.**	**Min**	**Max**	**Mean**	**St.dev.**	**Min**	**Max**
Pinus palustris	67294	48.02%	28.2	13.2	94.2	18.4	3.99	3.4	30.8	56	21.5	5	228
Pinus taeda	27481	19.61%	28.2	13.0	94.2	20.9	5.11	3.7	39.3	41	17.4	11	150
Pinus elliottii	11158	7.96%	25.2	7.9	64.8	20.1	3.57	8.2	31.7	36	6.7	14	85
Pinus serotina	5854	4.18%	30.6	13.5	78.6	20.2	5.14	6.1	37.8	54	23.8	13	212
Quercus laevis	4199	3.00%	15.0	9.2	81.6	20.9	5.39	17.1	24.7	50	21.2	35	65
Quercus marilandica	4194	2.99%	18.6	8.6	64.2	19.5				29	0.0	29	29
Nyssa sylvatica	2809	2.00%	26.4	12.1	100.2	19.2				91	0.0	91	91
Acer rubrum	2597	1.85%	20.4	11.2	78.6								
Quercus falcata	2023	1.44%	28.2	16.7	106.2	20.2	6.05	13.4	25.0	82	25.6	58	109
Liriodendron tulipifera	1898	1.35%	34.8	15.8	94.2	32.3				90	0.0	90	90
Quercus stellata	1882	1.34%	22.8	12.8	84.6								
Liquidambar styraciflua	1818	1.30%	24.6	11.6	80.4								
Carya sp.	963	0.69%	22.8	11.4	75.6								
Quercus nigra	809	0.58%	20.4	12.6	82.8								
Pinus echinata	737	0.53%	24.6	12.5	66.6	20.0	4.02	11.0	28.0	60	25.9	22	154
Nyssa sylvatica	725	0.52%	23.4	10.9	60.0								
Quercus velutina	723	0.52%	28.8	14.9	78.0								
Cornus florida	478	0.34%	10.8	4.2	38.4								
Chamaecyparis thyoides	449	0.32%	29.4	13.4	111.0	27.7				70	0.0	70	70
Quercus rubra	308	0.22%	27.6	13.6	75.0	12.8				48	0.0	48	48
Quercus alba	281	0.20%	25.2	16.5	133.9								
Taxodium distichum	276	0.20%	36.6	18.2	156.7								
Quercus incana	217	0.15%	16.2	8.8	55.2								
Ilex opaca	130	0.09%	13.2	6.5	46.8								
Prunus serotina	129	0.09%	18.0	8.9	49.8								
Magnolia virginiana	92	0.07%	10.8	6.4	43.2								
Oxydendrum arboreum	76	0.05%	13.8	7.7	41.4								

Pinus virginiana	70	0.05%	22.8	15.7	75.0	17.1	4.01	10.7	20.4	39	20.8	16	72
Quercus phellos	64	0.05%	16.2	9.7	42.0								
Diospyros virginiana	55	0.04%	15.0	13.6	94.2								
Juniperus virginiana	46	0.03%	27.0	14.5	54.0								
Salix sp.	37	0.03%	13.8	6.7	31.8								
Magnolia grandiflora	34	0.02%	11.4	6.4	30.0								
Quercus virginiana	32	0.02%	32.4	19.1	78.0								
Platanus occidentalis	31	0.02%	30.0	16.6	67.8								
Fraxinus pennsylvanica	30	0.02%	23.4	11.2	53.4								
Betula nigra	19	0.01%	31.2	17.0	64.8								
Ulmus sp.	16	0.01%	18.0	11.9	53.4								
Quercus michauxii	14	0.01%	27.0	8.3	40.8								
Sassafras albidum	12	0.01%	16.8	10.2	33.6								
Quercus sp.	10	0.01%	12.0	8.4	34.2								
Morus sp.	8	0.01%	19.2	8.5	36.6								
Crataegus sp.	7	0.00%	9.0	1.6	11.4								
Persea borbonia	7	0.00%	6.6	1.1	8.4								
Carpinus caroliniana	6	0.00%	11.4	3.5	14.4								
Juglans nigra	5	0.00%	31.2	17.0	51.0								
Quercus coccinea	4	0.00%	23.4	11.5	35.4								
Taxodium distichum	2	0.00%	31.8	6.4	36.6								
Melia azedarach	2	0.00%	18.0	15.1	28.8								
Carya illinoensis	1	0.00%	24.0										
Carya tomentosa	1	0.00%	16.8										
Prunus sp.	1	0.00%	26.4										
Tilia americana	1	0.00%	28.8										

Table IV.2 – Results from the year 2000 inventory in Fort Bragg.

Evaluation and re-calibration of submodels

Because we were primarily concerned with projection of large tree growth and mortality, we elected not to modify the establishment and small tree growth models on the Southern Variant. In addition, we restricted our species list to the common pines found on Fort Bragg: longleaf pine, loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* Engelm.), pond pine (*Pinus serotina* Michx.), and shortleaf pine (*Pinus echinata* Mill.). Although over 50 tree species occur on Fort Bragg, non-pine species are typically a minor component of the upland stands that comprise most of the forest [Figure 46]. Most stands are regenerated naturally, but all of the slash pine is in plantations.

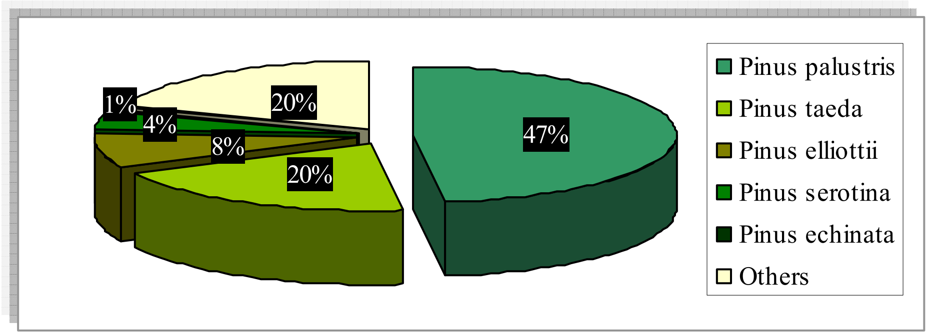


Figure 46 – Relative abundance of pine species in the Fort Bragg database.

Our original work plan called for evaluation of the existing submodels in the Southern Variant, using the Fort Bragg data as a validation data set (see also Canavan, 1997; Smith-Mateja and Ramm, 2002). We intended to re-fit only the submodels that performed poorly against the Fort Bragg data. However, our experience with some of the simple submodels (e.g., height dubbing, which is discussed below) indicated that it would be more efficient to approach each submodel with the intent of re-fitting it with Fort Bragg data. Evaluation of the submodels, as parameterized in the Southern variant, would be done primarily to quantify the difference between submodel versions.

We developed a standard methodology for evaluating FVS submodels and reporting the results according to the following steps:

- ☐ Introduction
  - Species analysis
  - Existing literature about submodel (general and for species of interest)
  - Characteristics of FVS submodel:
    1. model logic and form
    2. parameter values
    3. default goodness of fit (if provided)

  - Variables of interest:
    1. field protocol
    2. descriptive statistics
    3. missing values and outlier flagging

- ☐ Model evaluation
  - Run simulation:
    1. insert default parameter values
    2. filter data according to model assumptions
    3. enter model equation
    4. compute predicted values and residuals
  - Plot model against observation points
  - Residual analysis:
    1. descriptive statistics
    2. plot histogram (mean prediction bias)
    3. test for normality of distribution
    4. plot against dependent variable (observed vs. predicted, testing for model form bias)
    5. plot against independent variable(s)

6. plot against other variables of interest not included in the model (site-related bias), e.g., tree size, age/increment, plot and stand descriptors

- Interpretation (are biases substantial and/or systematic?)

☐ Model re-calibration

- Fit parameters for new model(s) – using same model form – and estimate goodness of fit
- Evaluate collinearity
- Calculate confidence intervals for new parameters
- Between-model comparison of goodness-of-fit and confidence intervals for fitted parameters
- Plot predicted values vs. observations and FVS default predictions
- Residual analysis for re-calibrated model

☐ Conclusions

- Consider biases and possible causes/resolutions:
    1. outliers (evaluate leverage/influence)
    2. data filtering
    3. test for normality, homoscedascicity
    4. option for keyword-based recalibration
    5. include stochastic components
    6. modify model logic
    7. implement new model form according to literature
    8. include new variables when influential according to residual plots/literature
- Discussion on model performance
- Recommendations for sampling

The validation runs used version 6.2 of the FVS-SN variant with a revision date of 30/01/2006. FVS variants are continuously being updated and improved. These same data runs through a current version of the model would yield different results.

Height Dubbing Submodel

Fitting the simple submodels, such as those used for dubbing missing tree parameters, to Fort Bragg data was straightforward. For example, the height-dubbing submodel of the Southern Variant predicts mean total tree height for a given diameter at breast height and species. Since Meyer (1940), this has been one of the most studied relationship in forestry (Zeide and Vanderschaaf, 2002). Several functions to model the relationship between breast-height diameter and total height of the trees in a stand have been used (Curtis, 1967; Monserud, 1975; Ek et al., 1984; Larsen and Hann, 1987; Parresol, 1992; Huang et al., 1992; Flewelling and de Jong, 1994; Zhang, 1997; Fang and Bailey, 1998; Lopez Sanchez et al., 2003). Theoretical and empirical studies suggest that height is an allometric function of diameter to the ⅔-th power (Greenhill, 1881; McMahon, 1973; Norberg, 1988; O'Brien et al., 1995), due to elastic similarity and the need to maintain a constant safety factor against both buckling and bending due to tree weight (McMahon and Bonner, 1983; Rich et al., 1986).

Height-diameter curves should pass through the origin and have a positive slope that approaches zero as diameter becomes larger (Curtis, 1967). Logically constraining the height-diameter curve to pass through (0, 1.3) is important when measurements include very young trees. Linear models (Curtis, 1967) can be easily fitted, especially if data sets are small and do not represent the full range of the diameter distribution. However, when linear models contain a logarithmically transformed response variable, they introduce some log bias that should be corrected (Baskerville, 1972; Dolph et al., 1995; Payandeh, 1981). Yet this correction cannot be performed if the residuals are not normally distributed (Baskerville, 1972; Bell et al., 1981), and the choice of alternative correction factors is not always easy (Flewelling and Pienaar, 1981).

The main advantage of the nonlinear models is that their flexibility allows biologically reasonable shapes (Huang et al., 1992). This feature is highly desirable because users often extrapolate them (Vanclay, 1994). Their are less affected by outliers (Batista et al., 2001); also, they do not require any log bias correction, although nonlinear height diameter curves often need to be weighted to correct for departures from homoscedasticity (Neter and Wasserman, 1974). A weighted regression approach with (*Dbh – N*) as the weight has been often used, with N ranging from 0 to 4 (e.g., Garman et al., 1995; Gonda et al., 2004).

The selection of a functional form for height-diameter relationships should not be restricted to the ease-of-fit to data, nor only to data-related criteria, but also should consider characteristics of the chosen model, such as (1) monotonic increment, (2) inflection point, and (3) asymptote (Parresol, 1992; Yuancai and Parresol, 2001) [Figure 47]. Height-diameter equations based on non-asymptotic functions (Larsen and Hann, 1987; Wang and Hann, 1988 and references therein) and second-order polynomial equations (e.g., McDonald, 1983; Dale and Hemstrom, 1984) provide reasonable predictions when tree sizes fall within the diameter range of the data used to generate equation coefficients, but because of their mathematical form they are deficient for extrapolations beyond the empirical data set (Garman et al., 1995). Asymptotic functions adequately fit height-diameter relationships over the range of observed data, constraining height increase above maximum observed values (Prentice and Helmisaari, 1991; Niklas, 1995). Height may be constrained by limitations of mechanical support (McMahon, 1973; Niklas, 1989), increasing respirational load of stem tissues, or water stress in the upper shoots of tall trees (Friend, 1993; Ryan and Yoder, 1997).

The curve of the functional form should be typical of a height cumulative growth curve, which starts at the origin value, increases steadily to attain maximum growth at an inflection point, and then gradually approaches an asymptotical value. Parresol (1992) argued that the S-shaped mode1 reflects appropriate biological properties that are not captured by the data-driven concave model, even if it may exhibit slightly poorer fit statistics. This type of curve is also directly compatible with a height-increment curve.

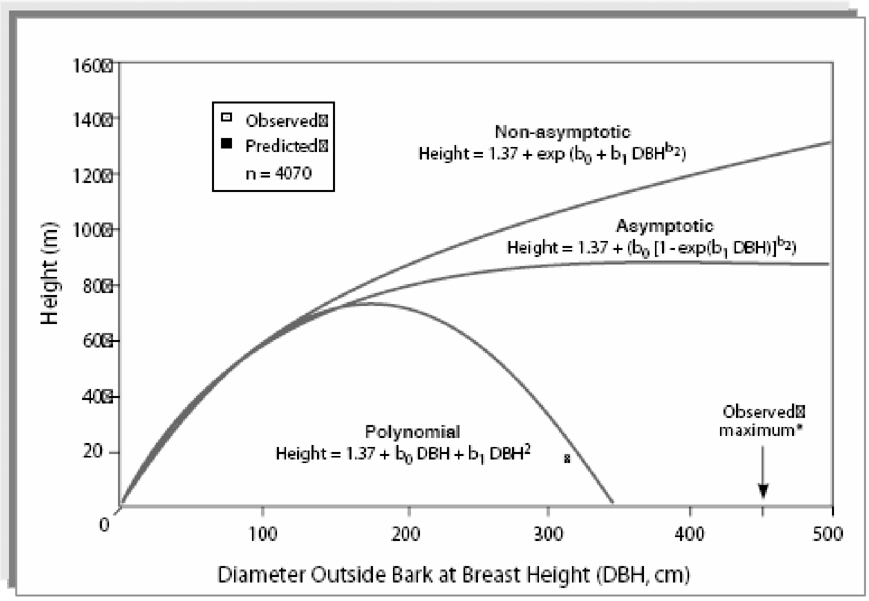
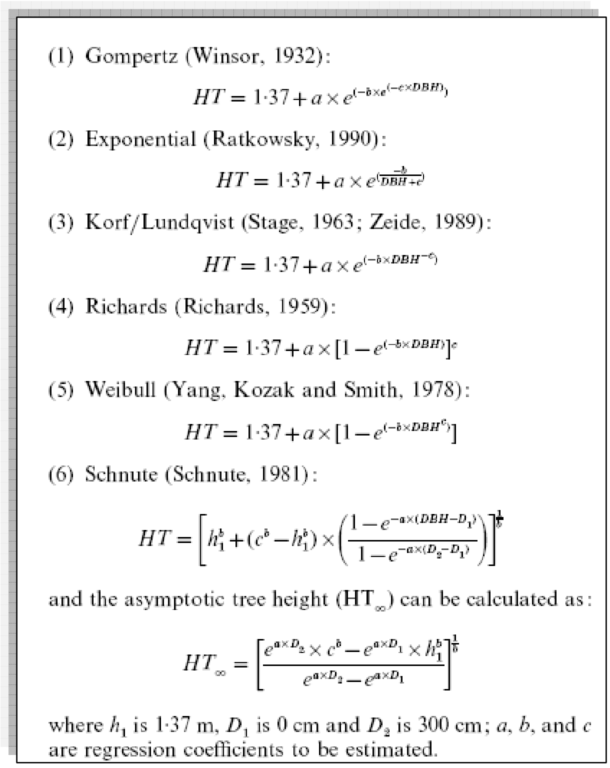


Figure 47 - Comparison of three height-diameter equation forms for Douglas-fir in the Northern Oregon Cascades region (from Waring and Franklin, 1979).

The most commonly recommended model is the Chapman-Richards (Richards, 1959) growth function (Huang et al., 1992; Garman et al., 1995; Zhang et al., 1996; Zhang, 1997; Fang and Bailey, 1998; Peng, 1999; Peng et al., 2001), based on its well-known flexibility and biologically interpretable coefficients (Pienaar and Turnbull, 1973). According to the literature, the six growth functions in Figure 48 have appropriate mathematical properties and promising prediction performance for tree height-diameter relationships (Brewer et al., 1985; Arabatzis and Burkhart, 1992; Huang et al., 1992; Zeide, 1993, Zhang, 1997).



(1) Gompertz (Winsor, 1932):

$$HT = 1{\cdot}37 + a \times e^{(-b \times e^{(-c \times DBH)})}$$

(2) Exponential (Ratkowsky, 1990):

$$HT = 1{\cdot}37 + a \times e^{(\frac{-b}{DBH+c})}$$

(3) Korf/Lundqvist (Stage, 1963; Zeide, 1989):

$$HT = 1{\cdot}37 + a \times e^{(-b \times DBH^{-c})}$$

(4) Richards (Richards, 1959):

$$HT = 1{\cdot}37 + a \times [1 - e^{(-b \times DBH)}]^{c}$$

(5) Weibull (Yang, Kozak and Smith, 1978):

$$HT = 1{\cdot}37 + a \times [1 - e^{(-b \times DBH^{c})}]$$

(6) Schnute (Schnute, 1981):

$$HT = \left[h_1^b + (c^b - h_1^b) \times \left(\frac{1 - e^{-a \times (DBH - D_1)}}{1 - e^{-a \times (D_2 - D_1)}}\right)\right]^{\frac{1}{b}}$$

and the asymptotic tree height (HT_∞) can be calculated as:

$$HT_\infty = \left[\frac{e^{a \times D_2} \times c^b - e^{a \times D_1} \times h_1^b}{e^{a \times D_2} - e^{a \times D_1}}\right]^{\frac{1}{b}}$$

where h_1 is 1·37 m, D_1 is 0 cm and D_2 is 300 cm; a, b, and c are regression coefficients to be estimated.

Figure 48 – Six asymptotic HD models (from Zhang, 1997, references therein).

Sources of variability

The height curves obtained for stands do not adapt well to all the possible situations that can be found within stands of that species. This is for a number of reasons (Lopez Sanchez et al., 2003):

1. The height curve of an even-aged stand does not remain constant in time (Curtis, 1967) and is displaced in an increasing direction, for both variables, with age (i.e., trees that have the same diameter at different times belong to sociologically different classes). Moreover, as tree form and allometry are influenced by both environmental and competitive factors (Holbrook and Putz, 1989), temporal changes in these

conditions are likely to affect the diameter–height relationship. In mixed-species natural stands, species differences in relative shade tolerance and successional status will result in differences, over time, in the abundance and range of tree sizes observed for each species. This may cause varied uncertainty among species in estimating diameter–height relationships at any given time (Ishii et al., 2000). Stand age is suggested not to improve the model significantly (Zhang et al., 1997; Jarayaman and Lappi, 2001). Nevertheless, if the model is used to predict the evolution of the stand in time, this requires the inclusion of a temporary variable. This can be achieved in an indirect way by developing temporal models for the exogenous variables, such as dominant height or diametric distribution, or modeling the changes in the height-diameter relationship over time (Kohyama et al., 1990).

2. The relation varies from one stand to another, depending on site conditions: the height curves for good quality sites will have steeper slopes than those for poor quality sites (Garman et al., 1995; Fulton, 1999). Moreover, for a particular height, trees that grow in high density stands will have smaller diameters than those growing in less dense stands, because of greater competition among individuals. The effects of environmental conditions and competitive interaction on diameter–height relationships are well documented (e.g., Ritchie and Hann, 1986; Hann and Ritchie, 1988; Krumland and Wensel, 1988).

Development of general models that for a wide range of geographical validity connect tree height and diameter has been approached from different perspectives:

I. Two-stage approach (Ferguson and Leech, 1978). The height–diameter relationship is first fitted individually for each sampling unit (plot, stand). In a second stage, parameters are explained using stand variables such as density, basal area, dominant height, age, and dominant diameter as covariates (Krumland and Wensel, 1978; Larsen and Hann, 1987; Parresol, 1992).

II. Development of single models for different geographical or ecological regions, or inclusion of regional effects in the model as categorical variables (Fulton, 1999; Huang et al., 2000; Peng et al., 2004).

III. Analysis of the spatial pattern of variability in height/diameter ratio and geostatistical modeling of the parameters (Nanos, 2001).

IV. Use of models with random coefficients, which define a fixed population average response, including varying random parameters for each sampling unit (Hökkä, 1997; Lappi, 1997; Jayaraman and Lappi, 2001). Robinson and Wykoff (2004) used stand and point identifiers as random effects. The fixed-effects parameters alone can be used to obtain the "average" height-dbh curve based on all stands. Calibration of a height-dbh model for one particular stand estimates random parameters for the stand of interest, together with estimates of the fixed-effects parameters, the residual variance, and the estimated variance-covariance matrix for the random-effects parameters. Robinson (1991) presents a highly readable account, and Pinheiro and Bates (2000) presents a detailed presentation of these models and their fitting.

Influential variables

To improve height predictions and to adjust for differences between stands, foresters have used additional independent variables such as age (Curtis, 1967), site index, and basal area (Larsen and Hann, 1987; Wang and Hann, 1988) in their height-diameter equations. Dominant height (Krumland and Wensel, 1978; Larsen and Hann, 1987; Cañadas, 2000), density (Nanos, 2001; Zhang et al., 1997) and a measurement of the dispersion in the diameter distribution (Fang and Bailey, 1998) can be included as covariates. Density and dominant height have been found to be positively correlated with height. Dominant height correlation means that a relation exists between site index and stand height, as demonstrated by Eichorn's rule (Eichorn, 1902). The relation between density and height is shown by the fact that for the same height, trees located in denser stands have smaller diameters than those located in less populated stands, or, in other words, the height/diameter ratio is higher in denser stands (Zeide and Vanderschaaf, 2002).

Krumland and Wensel (1988) and Hanus et al. (1999a, 1999b), used diameter and height referred to the 100 biggest trees in the stands rather then fitting to all the tree measurements. Their model accounts for the tendency of even-aged pure stands to have a tighter H-D relationship than uneven-aged or mixed stands by constraining the H-D curve to equal H_{100} when D equals D_{100} and also by scaling the projected H-D ratio to the observed H_{100}:D_{100} relationship.

Sample size

The model has been fitted with any range of observation units, from 18 (Colbert et al., 2002) to tens of thousand (Lopez Sanchez et al., 2003; Peng et al., 2004). Krumland and Wensel (1978) proposed the measurement of the height of four dominant trees per plot to calibrate height–diameter relationship for different species in California. Houghton and Gregoire (1993) compared several sampling designs and subsample size, finding the best results with a purposive sample (neither random nor systematic). Measurement of the height of the 20% largest trees in the plot has also been shown to be a useful approach (Calama and Montero 2004). Limited observation ranges need not translate into larger uncertainties in linear regression, but they can have extreme impact in fitting nonlinear models (Draper and Smith, 1988).

Excluding damaged and suppressed trees from the static diameter–height relationship usually increases predicted heights (Ishii et al., 2000); damage and shading can have variable effects on predicted height estimates depending on the species and on tree size.

Model form

Very few models have been found in literature for the height-diameter relationship of the main pine species in Fort Bragg:

[15] $$H = 1.3 + \left(p_2 - 1.3\right)\left(1 - e^{-p_3 D}\right) + \varepsilon$$

(calibrated on 55 Longleaf pine observations in Texas by a maximum likelihood approach [Fulton, 1999]);

[16] $$H = p_0 + p_1 D$$

(calibrated on 82 Loblolly and Shortleaf dominant pine observations in Texas [Oswald et al., 2002]);

[17] $$H = 1.3 + p_2 \left(1 - e^{-p_3 D}\right)^{\mathrm{p}_4}$$

(calibrated for Slash pine [Pienaar, 1991]).

If some or all tree records in a FVS input tree list file have a height measurement missing, FVS will estimate the missing height using either the height-diameter relationships of the Curtis-Arney equation [18] (Curtis, 1967; Arney, 1985), or, the Wykoff equation [19] (Wykoff et al., 1982) form. The only time the Wykoff equation is used to estimate missing heights is if the model goes through self-calibration: the model will automatically calibrate height for a particular species if there are at least 3 height measurements for that species.

$$H = 1.3 + p_2 e^{-p_3 D^{p4}} \qquad [18]$$

$$H = 1.3 + e^{b_0 + b_1\left(\frac{1}{D+1}\right)} \qquad [19]$$

where H is tree height,

D is tree diameter at breast height,

$p_0 \ldots p_4$ are model parameters [Table IV.3].

The Curtis-Arney model, sometimes called the Lundqvist or the Korf equation (Zeide, 1989, 1993), represents the exponential generalization of the allometric equation (Arabatzis and Burkhart, 1992; Thomas, 1996) and is similar (but not equal) to the original Chapman-Richards (1959) formulation. Parameter p_2 is the model estimate of maximum attainable height for the species; the exponent ranges from -4 to 2, with vales between -1 and 1 being the most common ones (Gonda et al., 2004). Variability in the HD relationship for different tree size or age (Curtis, 1967) is accounted for by a linear combination between the Curtis-Arney model and a linear equation for trees smaller than 7.5 cm in dbh:

$$H = 1.31 + \frac{\left(1.3 + p_2 e^{-3^{p4} p_3}\right)\left(D - D_{BW}\right)}{3 - D_{BW}} \qquad [20]$$

where D_{BW} is the nominal bud width diameter at 1.3 m.

Species	p_2	p_3	p_4	D_{BW}	b_0	b_1	R^2_{Wykoff}
Shortleaf pine	444.092	4.1188	-0.3062	0.5	4.627	-6.4095	0.6518
Slash pine	1087.101	5.1045	-0.2428	0.5	4.656	-6.2258	0.796
Lonleaf pine	98.561	3.8993	-0.8673	0.5	4.599	-5.9111	0.7551
Pond pine	142.747	3.9726	-0.5871	0.5	4.546	-6.8	0.8553
Loblolly pine	243.861	4.2846	-0.4713	0.5	4.690	-6.8801	0.7242

Table IV.3 – Coefficients for the Curtis-Arney equation (Imperial units) for the species of interest according to the FVS-SN (Donnelly et al., 2001).

To reflect local conditions, measured height and diameter data for trees with dbh ≥ 12.5 cm and no indication of a broken or damaged top are used to adjust the b_0 parameter of the Wykoff equation (i.e., the intercept of the log-transformed linear model). Holding the slope constant while allowing the intercept to vary captured some of the local variation and minimized the risk of instability (Robinson and Wykoff, 2004). The imputed height is then a compromise between the lack of local variation in a global model and the limited power of local data to provide useful estimates of model parameters. This approach appears to work reasonably well, but no rigorous evaluation has been attempted, and no alternatives were explored (Robinson and Wykoff, 2004).

According to Robinson and Wykoff (2004), fitting the model to the data is better than using a published model, as long as the fitting takes full advantage of the available data. Since mostry mature trees were represented in the database, we chose as the object of the re-calibration only the Curtis-Arney submodel for big trees and the Wykoff equation with the default intercept and slope.

Results

After deletion of null observation and flagging of likely outliers (i.e., records with a H/D ratio lower than 25 or higher than 150), a total of 11,260 dbh measurements and 11,254 height measurements were included in the validation database for the 5 species of interest [Table IV.4]. Frequency distributions were normal for all the analyzed species, except for the Pond pine and Shortleaf pine dbh distributions (Kolmogorov-Smirnov test), presumably due to the limited sample size.

	Diameter [cm]					**Height [m]**				
	N	**mean**	**min**	**max**	**dev.st**	**N**	**mean**	**min**	**max**	**dev.st**
Loblolly	2403	5.2	0.9	13.2	1.67	2401	20.8	3.7	39.3	5.11
Longleaf	7302	5.3	0.9	10.5	1.57	7298	18.4	3.4	30.8	3.99
Pond	489	5.5	1.5	13.1	1.81	489	20.3	6.1	37.8	5.15
Shortleaf	74	5.1	2.2	8.9	1.48	74	19.9	11.0	28.0	4.02
Slash	992	4.4	2.0	9.9	0.98	992	20.1	8.2	31.7	3.56

Table IV.4 –Validation dataset for the pine species of interest.

Evaluation of the embedded submodels evidenced that both of them averagely overpredicted tree height for all species except pond pine; the mean bias ranged from 0.32 to 2.52 m [Table IV.5]. The distortion caused by use of the default model were severe especially for Longleaf pine; since this species was represented by a great number of observations, we inferred overprediction to be systematic, and witnessed residuals as high as 19.6 m in magnitude. The Wykoff uncalibrated model did not perform consistently better that the Curtis-Arney equation.

Table IV.5 – Residual statistics [m] for tree heights modeled by the default Curtis-Arney and Wykoff submodels embedded in FVS-SN.

			Curtis-Arney	**Wykoff.Uncalibrated**
Loblolly pine	N	Valid	2401	2392
		Missing	0	9
	Mean bias		0.90	0.32
	RMSE		1.11	1.09
	Min		-14.27	-14.56
	Max		13.85	13.37
Longleaf pine	N	Valid	7298	7236
		Missing	0	62
	Mean bias		2.36	2.52
	RMSE		1.11	1.14
	Min		-7.83	-7.52
	Max		19.25	19.63
Pond pine	N	Valid	489	487
		Missing	0	2
	Mean bias		-0.76	-1.29
	RMSE		1.01	1.10
	Min		-11.81	-13.62
	Max		8.72	8.10
Shortleaf pine	N	Valid	74	74
		Missing	0	0
	Mean bias		1.73	0.60
	RMSE		0.94	0.82
	Min		-4.09	-4.92
	Max		8.99	6.91
Slash pine	N	Valid	992	992
		Missing	0	0
	Mean bias		0.59	0.32
	RMSE		0.79	0.77
	Min		-6.32	-7.90
	Max		10.20	10.41

In addition, height prediction bias varied widely across the range of stem diameter, and decreased from over- to underpredicted values with increasing stand density and decreasing crown ratio class [Figure 49].

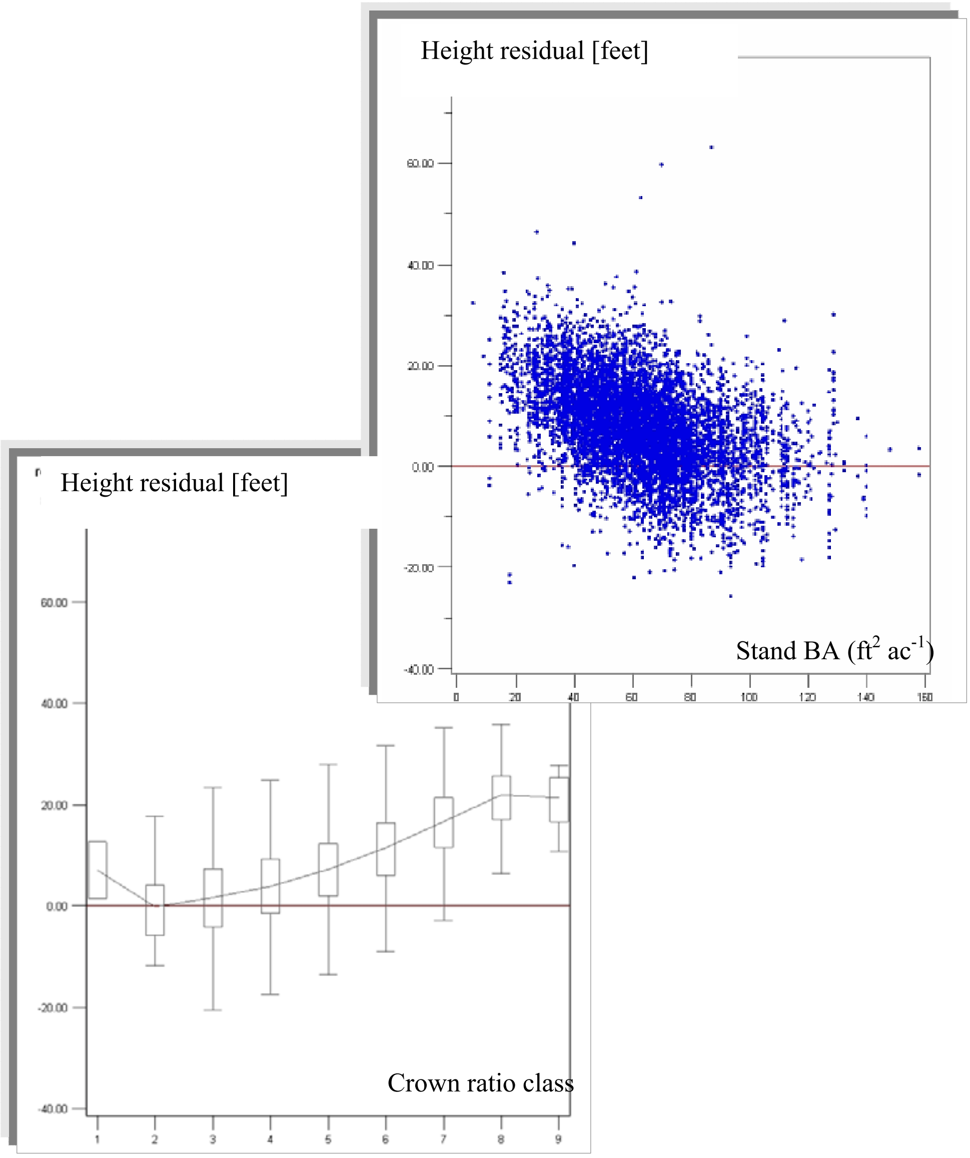


Figure 49 – Height prediction bias as a function of (a) stand basal area; (b) crown ratio class for Longleaf pine (uncalibrated Curtis-Arney model).

We found that substantial improvements in model performance were gained by re-fitting the Curtis-Arney equation. Average bias was reduced to zero, as was expected by the data-driven calibration, and minimum and maximum residuals were trimmed to less extreme values (up to +17.5 m) [Figure 50]. Conversely, the bias against tree density did not improve much, even if the error resulted generally modest for stand basal areas greater than 11.5 m^2 ha^{-1} (50 square feet per acre). Large overpredictions of height are the rule for open-grown trees, i.e., individuals with a live crown spanning on more than 70% of height. This could be fixed either including stand density or crown ratio in the variant model form, or by formulation of sampling recommendations imposing the measurement of height in open-grown trees (in order to avoid its model-based dubbing).

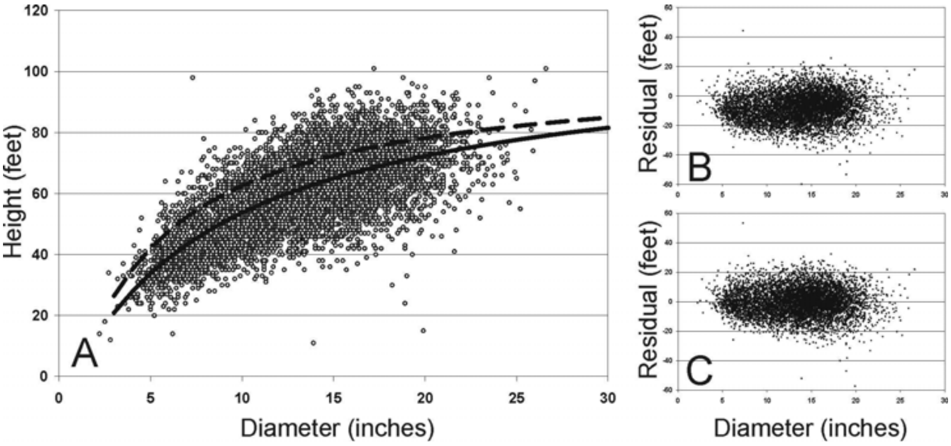


Figure 50 – Results of re-fitting the height dubbing model. A. Fort Bragg diameter-height data for 7371 longleaf pines. Dashed curve represents diameter-height relationship for longleaf pine in the Southern Variant, which has a mean bias of 2.36 m on Fort Bragg (B). Solid line represents re-fitted Curtis-Arney equation, whose mean bias is reduced to zero (C).

Diameter increment Submodel

Re-fitting the more complex models has required a different approach. For example, the diameter growth submodel for adult trees (dbh greater than 12.5 cm) uses a 14-coefficient equation with a mixture of categorical and continuous variables, some of which are logarithmically transformed and some of which are not [Table IV.6]. When this equation was fitted to the Fort Bragg data in its complete form, some coefficients were found to be non-significant or have improper sign (e.g., $b_6 > 0$, which suggests a positive relationship between tree diameter increment and plot basal area). In addition, our regressions yielded relatively low R^2 values, but the same was true for the FVS-SN regression to begin with, as reported by the variant manual (R^2 from 0.50 to 0.57 for the species of interest [Donnelly et al., 2001]).

	Variable	Description
ln(dds)* =	b_0	intercept
	$+ b_1 \cdot \ln \text{dbh}$	log of dbh (at beginning of estimation period)
	$+ b_2 \cdot \text{dbh}^2$	squared dbh
	$+ b_3 \cdot \ln \text{crwn}$	log of percent crown ratio
	$+ b_4 \cdot \text{hrel}$	relative height
	$+ b_5 \cdot \text{SI}$	site index for the species
	$+ b_6 \cdot \text{plttba}$	plot basal area
	$+ b_7 \cdot \text{pntbal}$	plot basal area in trees larger than subject tree
	$+ b_8 \cdot \tan \text{slp}$	tangent of slope in degrees
	$+ b_9 \cdot \text{f cos}$	tangent of slope, cosine of aspect
	$+ b_{10} \cdot \text{f sin}$	tangent of slope, sine of aspect
	$+ b_{11} \cdot \text{fortype}$	categorical variable for forest type group
	$+ b_{12} \cdot \text{ecounit}$	categorical variable for ecological unit group
	$+ b_{13} \cdot \text{plant}$	categorical variable for planted stands

* dds = (diameter inside bark at time_0 + periodic diameter growth$)^2$ – diameter inside bark^2 (Wykoff et al., 1982).

Table IV.6 – Variables and definitions in the FVS diameter growth submodel (from Donnelly et al., 2001).

In general, those factors thought to be influential in tree diameter growth fall into several categories. First is the category relating to the individual tree itself which consists of tree current diameter, height, and crown ratio. The second category relates to aggregate attributes of the tree's neighbors. In most cases this consists of stand or plot measures such as basal area per acre, basal area contained in all trees with larger diameter than the subject tree, and proportional height of the tree relative to the average height of the largest diameter trees in the stand. The third category relates to the site environment surrounding the tree. These factors are site index (or some similar fundamental measure of the site's productivity), the slope and aspect of the site, the site's forest type, and the site's location relative to the geographic range of all sites included in the variant (Donnelly et al., 2001). Because the ranges of some variables are relatively small on Fort Bragg as compared to the variability found within the geographic range encompassed by the Southern Variant, we anticipated that they may not be necessary components of the submodels at the local scale. For example, Fort Bragg has rolling terrain and the effects of slope and aspect on forest growth are not readily apparent. Slope position – e.g., moist bottomlands vs. dry ridges – is far more likely to influence stand growth than steepness or aspect. Because both moisture extremes are found on sites with relatively low slope values, any effect of slope on growth is likely to be confounded during equation fitting.

There are many ways users can make adjustments in an FVS simulation to produce more realistic results. Examples of this involves using serial correlation of diameter growth error and self-calibration of growth predictions based on user-provided increment data (Dixon, 2006). None of these were taken into account in the present analysis, that was aimed at assessing the predictive power of the basic growth model form used by the Southern variant.

In order to assess the role of each independent variable in predicting diameter increment for trees in Fort Bragg, we carried out a sensitivity analysis of model output (SA) of the diameter increment SN submodel. Global sensitivity analysis is the study of how the uncertainty in the output of a model (numerical or otherwise) can be apportioned to different sources of uncertainty in the model input (Saltelli et al., 2004). These studies may reveal model components with low and high sensitivity, both of which are of interest. Insensitive components may contribute little toward model predictions and could be targets for omission from the model during model revisions. Conversely, it is useful to know about model components with high sensitivity, because these may have the greatest impact on model predictions (Vanclay and Skovsgaard, 1997).

Most SA approaches to date have relied on local sensitivity analysis. This consists in evaluating the effect on model outputs exerted by individually varying only one of the model inputs across its entire range of plausible values, while holding all other inputs at their nominal or base-case values (Cullen and Frey, 1999). The difference in the model output due to the change in the input variable is referred to as the sensitivity of the model to that particular input variable (Morgan and Henrion, 1990). A major drawback of this method is that the sensitivity of the output to a given input may depend on interactions with other inputs, which are not considered. Thus, the results of nominal range sensitivity are potentially misleading, especially for multilinear and nonlinear models (Frey and Patil, 2002).

Hamilton (1997) proposed what he called “sensitivity analysis” of the FVS suite aa a whole. His method was based upon *a priori* alteration of each submodel’s output, by means of FVS keywords such as BAIMULT, HTGMULT and MORTMULT. These instructions provide a way to arbitrarily introduce multiplicative perturbations in diameter increment, height growth and mortality rate for a given species (Van Dyck, 2006). The percent difference in terms of standing volume at the end of the modeling timestep, resulting from the introduction fixed perturbations in each of the submodel, represented the author’s chosen sensitivity metric.

We propose herein the use of proper first-order sensitivity indices, i.e., ones that express the part of variance of model output Y due to model input X_i (Saltelli et al., 2004), as a mean to assess, *for each submodel*, which of the input factors is mostly responsible for producing realizations of the output of interest in a given target region. Partitioning the variance of the objective function Y is one possible way of performing sensitivity analysis. Although several computational techniques have been proposed (see for example Frey and Patil, 2002), sampling-based approaches to uncertainty and sensitivity analysis are both effective and widely used. Analyses of this type involve generating via Monte Carlo simulations a set of model evaluations Y_i (i = 1… N), corresponding to N different sampled values X_i of the vector $X = f(X_1,X_{2,\ldots}X_k)$ of input factors, and subsequently mapping uncertain analysis inputs to uncertain analysis results. The primary steps involved in conducting such a sensitivity analysis are the following (Helton, 2005):

1. Definition of probability distributions to characterize uncertainty in analysis inputs;
2. Generation of samples from uncertain analysis inputs;
3. Propagation of sampled inputs through model simulation;
4. Presentation of uncertainty analysis results;
5. Determination of sensitivity analysis results.

The complexity of biological systems is reflected by the presence in simulation models of both stochastic (i.e., aleatory) uncertainty and subjective (i.e., epistemic) uncertainty (Helton and Davis, 2001). Stochastic uncertainty arises because the system under study can behave in many different ways and thus is a property of the system (i.e., it relates to model form). Subjective uncertainty arises from an inability to specify the exact value of a quantity that is assumed to have a fixed value within a particular analysis and thus is a property of the analysts carrying out the study (i.e., it relates to model parameters and to measurement errors). Since we are mainly interested in model parsimony, rather than in assessing error propagation through the model (which is the aim of uncertainty analysis), our initial step was to consider only the first one as a source of model output uncertainty[22]. Therefore, we adopted the default SN submodel as the function to evaluate, retaining its original parametrization and evaluating uncertainty of each factor as its potential variability as computed by field measurements in Fort Bragg. [Table IV.7].

Input	**Definition**	**Distrib.**	**Range**	**Units**	**Notes**
dbh	Diam. breast height	Normal	2 - 30	In	
crwn	Live crown ratio	Normal	1 – 100	%	
h	Tree height	Normal	10 – 101	Feet	For *hrel* computation
H40	Height of 40 thickest trees ac^{-1}	Normal	40 – 140	Feet	
SI	Site Index	Normal	44 – 132	Feet	
BA	Basal area (stand)	Normal	5.5 – 158	feet^{2} ac^{-1}	
BAp	Basal area (plot)	Normal	10 – 270	feet^{2} ac^{-1}	For *pbal* computation
rank	%ile of tree's dbh in plot	Uniform	0 – 1	-	
slope	plot mean slope	Discrete	0 – 0.8	rad	
aspect	plot mean aspect	Uniform	0 – 2π	rad	
EUC	Ecological unit code	Constant	0	categ.	PVP232
forcode	Forest cover type	Discrete	0 – 1	categ.	From manual
plant	Plantation origin	Constant	0	binary	None in F.B.

Table IV.7 – Characterization of the input factors for SA of the diameter increment submodel.

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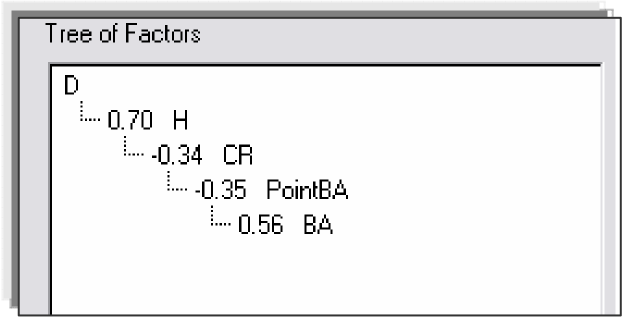
[22] Saltelli et al. (2004) defined the most general use of SA as being "concerned with model simplification, by fixing non-influential factors. The objective of this factor screening is to identify the factor or the subset of input factors that we can fix at any given value over their range of uncertainty without reducing significantly the output variance. If such set is identified, this means that the remaining factors explain practically all the unconditional variance."

The SIMLAB (2004) package was used for SA of the default dbh increment submodel in SN for Longleaf pine; 7302 individual measurements of this species were available from Fort Bragg inventory and were used to infer the shape, statistical properties (estimates of population mean and standard deviation) and range of each factor's probability density function (PDF). PDFs of sample variables were tested for normality by means of one-variable Kolmogorov-Smirnov test ($p < 0.05$) and truncated to minima and maxima measured in the field to avoid sampling outliers. Variables such as slope and forest type coding were assigned a discrete PDF with classes and weights inferred from sample frequencies, the former to overcome the irregularity of the measured variable's distribution, the latter to account for the growth correction coefficients assigned to different forest types by the variant manual (Donnelly et al., 2001).

The choice of the probabilistic sampling method was bound by the need of entering dependencies between input parameters. Pearson's correlation coefficients were computed from the dataset and entered in a dependence tree structure (Meeuwissen and Cooke, 1994) between tree dbh and height, tree height and crown ratio, crown ratio and stand basal area, and between the latter and plot basal area [Figure 51].



```
D
 └ 0.70  H
     └ -0.34  CR
         └ -0.35  PointBA
             └ 0.56  BA
```

Figure 51 – Correlation tree and Pearson's R between input factors as entered in SIMLAB.

Next, we generated a sample of elements from the distribution of the inputs previously specified. The desired correlation structure between input could only be analyzed by random or Latin Hypercube (LHS) sampling. Latin hypercube, or n-dimension stratified sampling [Figure 52], is very popular for use with computationally demanding models because its efficient stratification properties allow for the extraction of a large amount of uncertainty and sensitivity information with a relatively small sample size (Helton and Davis, 2003). Moreover, it performs better than simple random sampling when the output is dominated by a few components of the input factors (Iman et al., 1981).

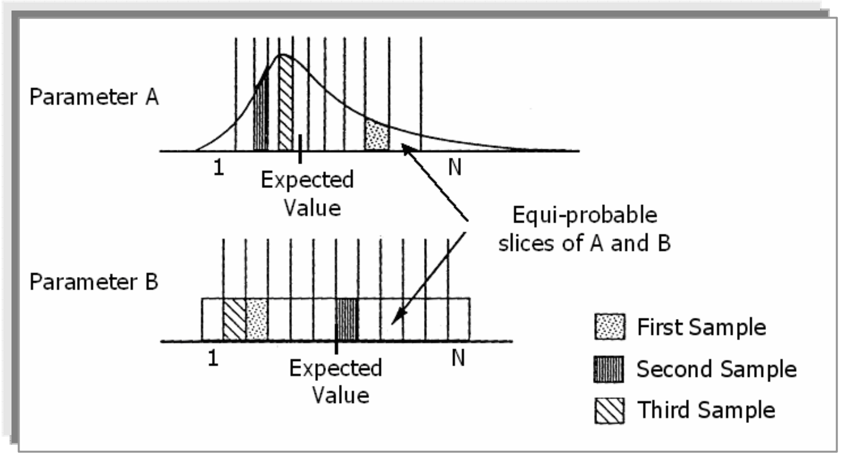


Figure 52 – Schematic Latin Hypercube Sampling technique for a hypothetical two-parameter model, modified from Tenhumberg et al. (2004). Probability density functions (PDFs) of model inputs were divided into N equi-probable intervals. For each simulation a value for each parameter combination was selected from one of these intervals at random, and without replacement.

Random sample generation in SIMLAB is implemented using an iterative function based on a user defined starting point (a 7 or more digit seed was entered). A number of 10,000 runs, much more than the suggested minima (3/2 or 4/3 times the number of factors [McKay et al., 1979]) was selected for the MonteCarlo simulation. The generated sample served as a starting point for model runs; the output whose sensitivity was first evaluated was *dds*, i.e., the change in squared inside-bark diameter [inches squared] during the estimation period[23].

In the model execution phase, each element of the sample is supplied to the model as input, and the corresponding model predictions are saved for use in later uncertainty and sensitivity analysis, performed by the Statistical Post Processor [Figure 53].

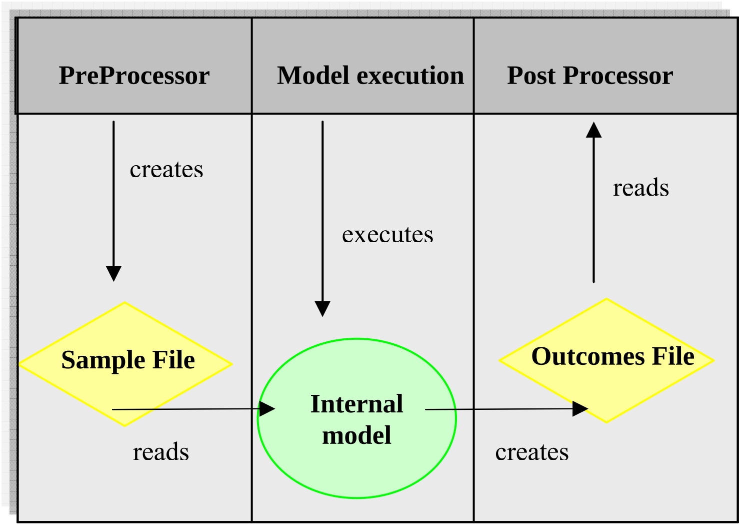


Figure 53 – Internal model execution schema (from EU IPSC, 2004).

Once a sample has been generated and propagated through the model, uncertainty analysis indices such as means, variances and distribution functions can be estimated directly from the model predictions, in order to determine the uncertainty in estimates for the dependent variables of interest. If the output

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[23] Running SA on the proper value of diameter increment requires calibration and analysis of the bark thickness submodel, which is the subject of ongoing research.

uncertainty is under an acceptable bound or within an acceptable range, then there is little reason to perform sensitivity analysis.

Figure 54 shows results of the 10,000 MonteCarlo-based model runs in terms of d_g, i.e., the estimated value of diameter growth inside bark [inches], which is obtained by the following equation:

$$d_g = \sqrt{dib^2 + dds} - dib \qquad [21]$$

where *dib* is tree dbh inside bark at the beginning af the modeling period [inches]; a constant ratio of 1.15 has been adopted as bark thickness coefficient for Longleaf pine, independently from tree size or age.

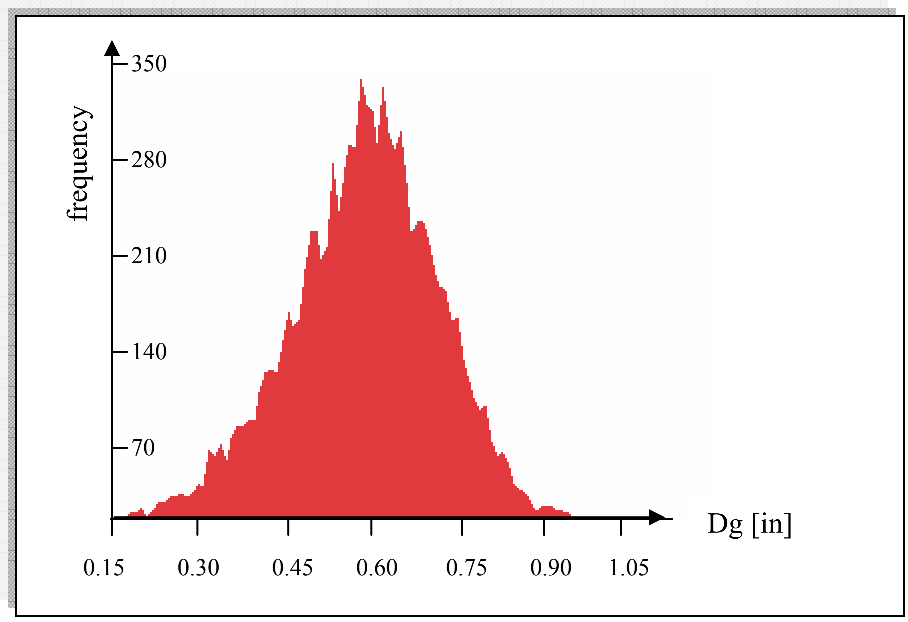


Figure 54 – Uncertainty analysis on model output.

Mean d_g was 0.58±0.12 inches (modeling step: 5 years), a value close to the average 5-year dbh increment measured on Longleaf pine woody cores in the year 2000 inventory, i.e., 0.57±0.27 inches. Modeled output is characterized by lower uncertainty than measured data, the latter having a wider and more skewed distribution (range: 0.08 to 2.36 inches, $g_1 = +1.403$). Hence, we were not worried about further reducing output uncertainty, but rather in better capturing the natural variability of diameter growth in Fort Bragg. SA proved useful to this regard, helping in prioritizing important factors and dumping unnecessary ones (i.e., not generating a significant part of output variability), in the framework of the look for a more comprehensive model form.

A number of approaches to sensitivity analysis can be used in conjunction with a sampling-based uncertainty analysis. The standardized regression coefficients β_j are a way to measure the sensitivity of Y to the factors X_j, in that they quantify the change in Y associated to a unit of change in a given parameter, all other remaining constant. The validity of the β's as a measure of sensitivity is conditional on the degree to which the regression model fits the data. Regression coefficients are described in Draper and Smith (1988) and their application to sensitivity analysis is reviewed by Helton (1993). In the rank-based version of the standardized regression coefficients, both the input and the output values are replaced by their ranks (Iman and Conover, 1979). Rank-based β_j's can be used for the purpose of model sensitivity analysis for nonlinear, albeit monotonic, models (Saltelli et al., 2000).

Partial correlation coefficients (PCC) provide a measure of the strength of the linear relationship between two variables after a correction has been made for the linear effects of other variables in the analysis. In other words, PCCs gives the strength of the correlation between Y and a given input X_j cleaned of any effect due to any correlation between X_j and any of the X_i, i not = j. In presence of correlation between factors, PCCs perform better than the simple Pearson's correlation coefficients. In particular PCCs provide a measure of variable importance that tends to exclude the effects of other variables (Conover, 1980;

Iman and Helton, 1988). The PCC can be computed on the ranks (Partial Rank Correlation Coefficients).

The use of sensitivity tests based on partition of data as the Smirnov two-sample test (Conover, 1980) exploits the idea of dividing the sample of the parameter Xj into two subsamples according to the quantiles of the output distribution Y. If the distributions of the two sub-samples mentioned above can be proved to be different then the parameter is an influential one; the Smirnov measure represents the maximum vertical distance between the two cumulative distribution frequencies that represent the subsamples' output. The three sensitivity measures evaluated in this study for the *dds* submodel with correlated input are resumed in Table IV.8.

Factor	**PRCC**	**SRRC**	**Smirnov**
D	0.770	0.652	0.552
H	0.453	0.282	0.469
CR	0.345	0.160	0.149
H40	-0.389	-0.163*	0.267
SI	0.489	0.216	0.316
BA	-0.292	-0.143*	0.277
PointBA	-0.240	-0.121*	0.292
rank	0.408	0.173	0.201
slope	0.095	0.037	0.169
aspect	-0.009	-0.003*	0.031
EUC		constant	
forcode	0.018	0.007	0.987
planted		constant	

*Table IV.8 – Partial rank regression coefficients (PRCC), Standard rank regression coefficients (SRRC) and Smirnov indices for the dds submodel. Indices marked by * are NOT significant at the 95% confidence level.*

Since the model presents non-linear features (e.g., calculation of *Hrel*), we chose to use rank SA indices. Diameter by large was the most important variablle followed by tree height, whose sensitivity indices showed further increase when correlations between input factors were introduced. This is consistent with evidence from growth modeling literature; the SN variant manual itself states that… "Dbh at the beginning of each projection cycle is usually the strongest single statistical determinant of diameter growth during the cycle" (Donnelly et al., 2001; see also Trasobares and Pukkala, 2004). Dbh has a strong proportional effect on *dds*, but this variable still has to go through square root transformation to reflect true increment; figure 55 shows the relationship between starting dbh, *dds* and *Dg* as a scatterplot resulting from 100 MonteCarlo simulations.

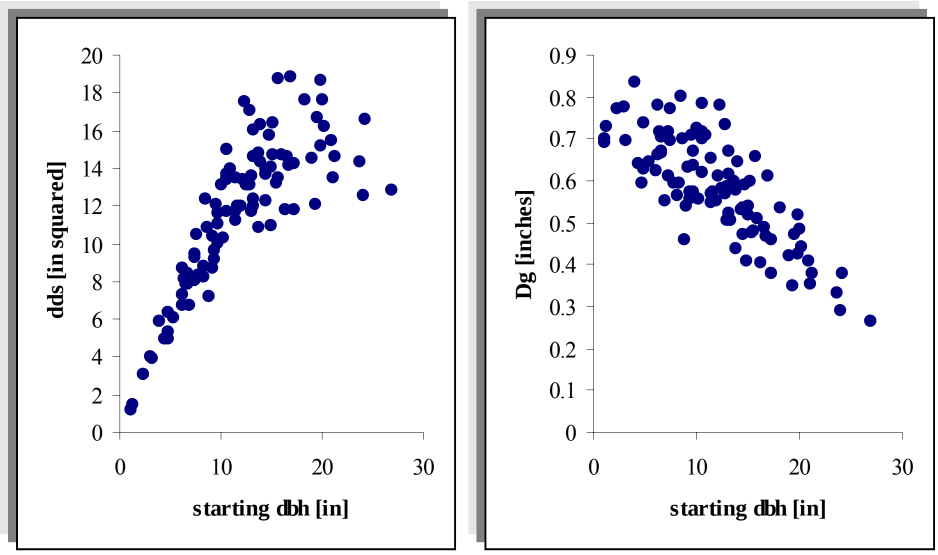


Figure 55 – Relationship between starting dbh, dds *and* Dg *obtained by 100 MonteCarlo-based model runs.*

Site Index and dbh ranking attain the third and fourth position in importance order. The signs of the SRRCs are consistent with expectations from ecologically sound growth behavior; surprisingly, none of the regression coefficients related to competitive influence resulted statistically significant. Slope unexpectedly shows a small but significant proportionality to growth, an effect that may be related to Fort Bragg morphology and Longleaf pine sites characteristics.

Forest code is not influential but, when different from Longleaf pine forest, determines significant differences in *dds* output (Smirnov test). For future re-engineering, some variables may be dropped because non influential (e.g. aspect, or EUC and plantation dummy variable which are constant for all records) for the considered database, or because they convey the same kind of information. In this later sense, just 1 competition measure among *Hrel*, BA and *PBAL* may be sufficient, to characterize neighbor influence.

The example reported in Figure 56 illustrates the amount of variability in diameter increment that is attributable to adding just plot basal area as a second predictor (after diameter) for dbh increment [22]. Adding basal area to the model made a small improvement in R^2 (0.65 vs. 0.73), but it reduced the magnitude of residuals by over 10 percent in some diameter classes.

$$[22] \qquad d_{percent} = \left(\mathrm{a} + \mathrm{b}BA\right)\left(\mathrm{c} - e^{-\mathrm{d}dbh}\right)$$

where $D_{percent}$ is 5-year diameter increment relative to starting dbh [in];

BA is plot basal area [feet ac^{-1}].

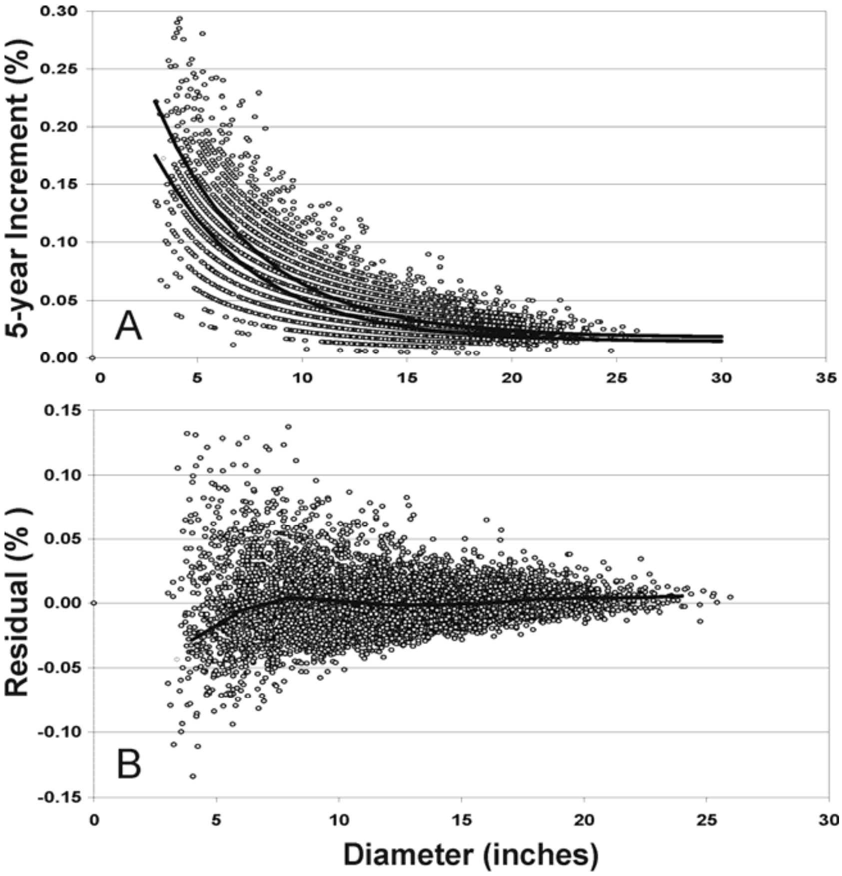


Figure 56 – Diameter growth data for longleaf pine. Diameter growth is shown as 5-year increment relative to starting diameter (A). Fitted lines in (A) show sensitivity of increment to plot-level density, from 30 ft^2 ac^{-1} (upper) to 110 ft^2 ac^{-1} (lower). Line through residual plot (B) shows residuals means for 2-inch diameter classes (2 to 24 inches).

Mortality Modeling

Perhaps the most challenging part of the model-building process will be development of the mortality submodels. The Southern Variant determines mortality rates using 2 mechanisms, depending on stand density index (SDI). When SDI < 55% of the maximum SDI for the forest type, FVS uses a background mortality rate that is a function of diameter and age. If SDI > 55%

of maximum SDI, then 2 different methods are used to calculate density-dependent mortality: 1) when stand quadratic mean diameter is lower than 10 inches, (annual) mortality rate varies according to how much SDI exceeds maximum SDI, and 2) when quadratic mean diameter is higher than 10 inches, mortality rate varies according to how much basal area exceeds maximum basal area for the forest type. The switch from SDI-mediated mortality to basal area-mediated mortality is evident if a stand in self-thinning condition (i.e., SDI > 55%) is projected in an FVS simulation [Figure 57].

However, the density-dependent self-thinning dynamic projected in the Southern Variant of FVS may not be realistic for mature longleaf pine stands. Recent work on stand density and dynamics of longleaf pine stands suggests that the expected self-thinning trajectory does not hold for stands with a quadratic mean diameter greater than about 10 inches (Shaw and Long, in press). Specifically, FVS projections of longleaf pine growth exceed the maximum limit of the size-density relationship, or “mature stand boundary”, proposed by Shaw and Long (in press) for longleaf throughout its range (Figure 57, Line A).

Size-density data from the 1990s and 2000s Fort Bragg inventories are consistent with the mature stand boundary for longleaf pine. Stands show a decrease in relative density with increasing mean diameter, and, for the largest stands, a decrease in basal area over time. This pattern indicates that factors other than density-dependent mortality, such as Zeide’s (2005) suggestion that mortality outpaces the re-occupation of released growing space, are actually limiting stand density.

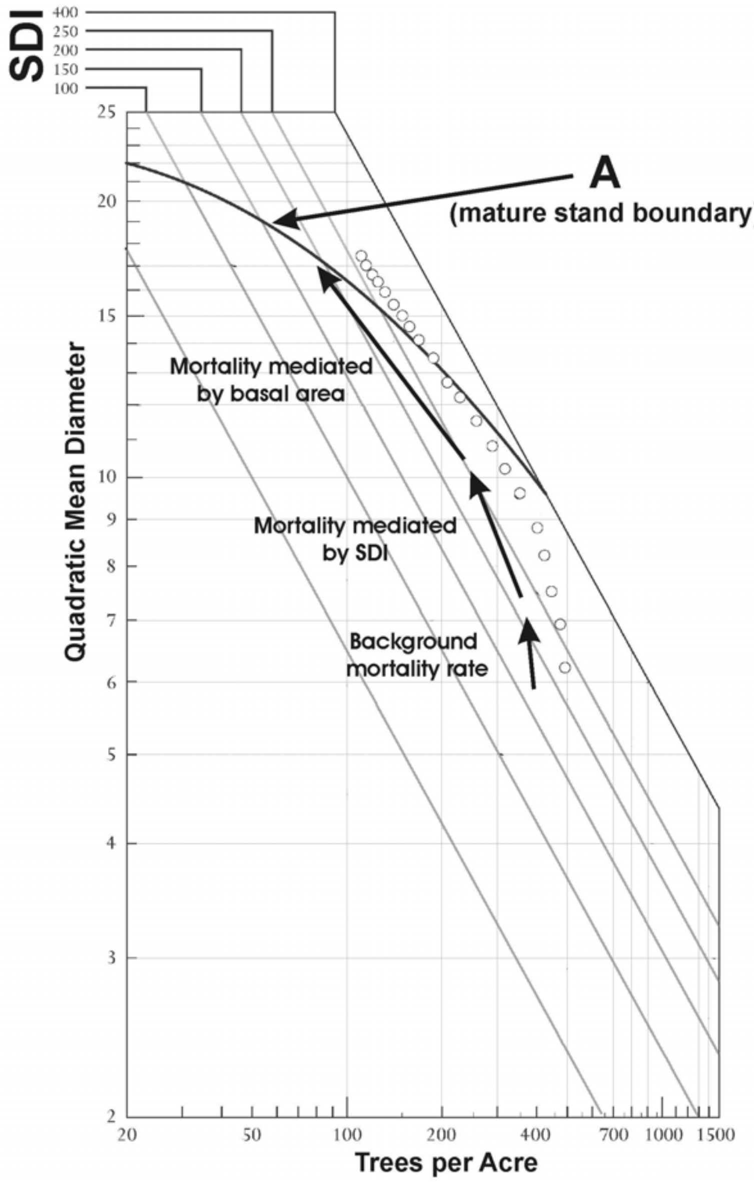


Figure 57 – Density management diagram for longleaf pine showing FVS projections of a natural longleaf pine stand from 25 to 125 years of age (open circles). The inflection in stand trajectory between 9 and 11 inches mean diameter results from the shift from SDI-mediated mortality to basal area-mediated mortality in the FVS mortality submodel. Line A is the mature stand boundary for longleaf pine proposed by Shaw and Long (in press).

It is possible to alter density-dependent stand dynamics “manually” in FVS. Users are allowed to supply their own maximum values for SDI and basal area using the SDIMAX and BAMAX keywords in FVS simulations (Van Dyck, 2006). It is also possible to modify mortality rates directly using the FIXMORT and MORTMULT keywords (Van Dyck, 2006). However, the general behavior of the mortality submodels is the same as with default values, making stand dynamics implied by the mature stand boundary difficult to emulate with keyword-based modifications. Also, keyword-based manipulation of stand growth and mortality is considered an inferior alternative to internal, fitted submodels because users often lack the data required to make meaningful changes to default values. Additional program logic would have to be included because different mechanisms limit stand density at different stages of stand development.

We will attempt to model the mature stand boundary using the existing FVS program logic and model forms. If stand dynamics cannot be modeled adequately using this approach, it may be necessary to modify program logic or form of mortality functions. Although the latter case may require fundamental changes to the FVS program code, some efficiency may be gained by developing a single mortality function that works for the entire range of mean diameter.

Conclusion

Additional work will be needed to run re-calibration and run sensitivity analysis of each FVS submodel and of the whole submodel chain, in order to get a deeper understanding of variables’ and submodels’ influence on final model outputs. This will involve testing the null hypothesis that each submodel is unbiased when applied to stands/conditions in a given locale (e.g., Ft. Bragg), against many different alternate hypotheses suggesting that some of the variables or model form used be held responsible for yield overpredictions. It has been shown that interactions between submodels can also play a significant role in propagating prediciton errors, such as the case of dbh modeling bias impacting average stand diameter and, consequently, triggering a shift in the way mortality is computed (Keyser and Stephens, 2002).

Although we have referred to this effort as development of a local FVS variant, the ultimate goal is to integrate the Fort Bragg submodels into the existing Southern Variant of FVS. This can be accomplished by establishing an administrative code for Fort Bragg, just as National Forests and Districts within National Forests are identified in existing FVS variants. A unique code for Fort Bragg would permit the use of appropriate parameters without alteration of FVS program logic, mostly by amending existing parameter arrays.

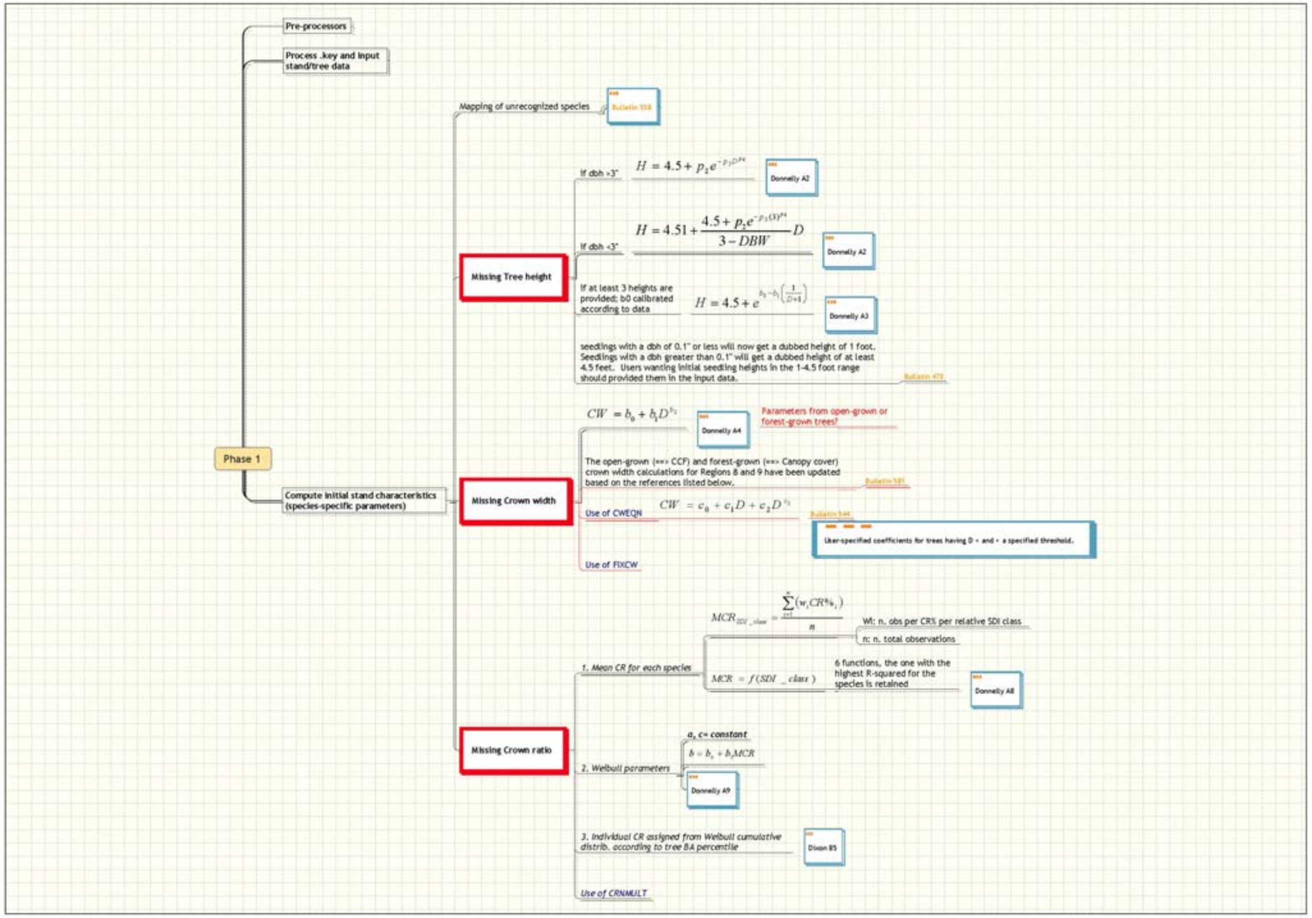
One potential obstacle to complete integration of the Fort Bragg submodels into the Southern Variant could be a situation where the model form used by FVS was found to be insufficiently flexible when applied to Fort Bragg data. In such a situation it may or may not be possible to integrate suitable models into the existing variant, depending on the degree to which a suitable solution would require modification of the FVS source code. The most likely place where this situation issue is likely to occur is in the case of the mortality submodel described earlier (for an application to a different growth modeling software, see Komarov et al., 2003). If, for example, the existing mortality submodel is found to be inadequate, there are 2 possible solutions: 1) create a stand-alone variant in which the model forms currently used in FVS have been modified, or 2) propose a comprehensive solution that would add more flexibility to current and future variants. The former solution is undesirable because it would create a variant that would be “frozen” in time and not maintained under the FVS framework – i.e., any updates to the variant would necessarily be initiated by Fort Bragg managers. The latter option would not only meet the goals for development of a variant suitable for Fort Bragg, but could potentially lead to improvements in performance of the Southern Variant by making more flexible submodels available for use in future updates.

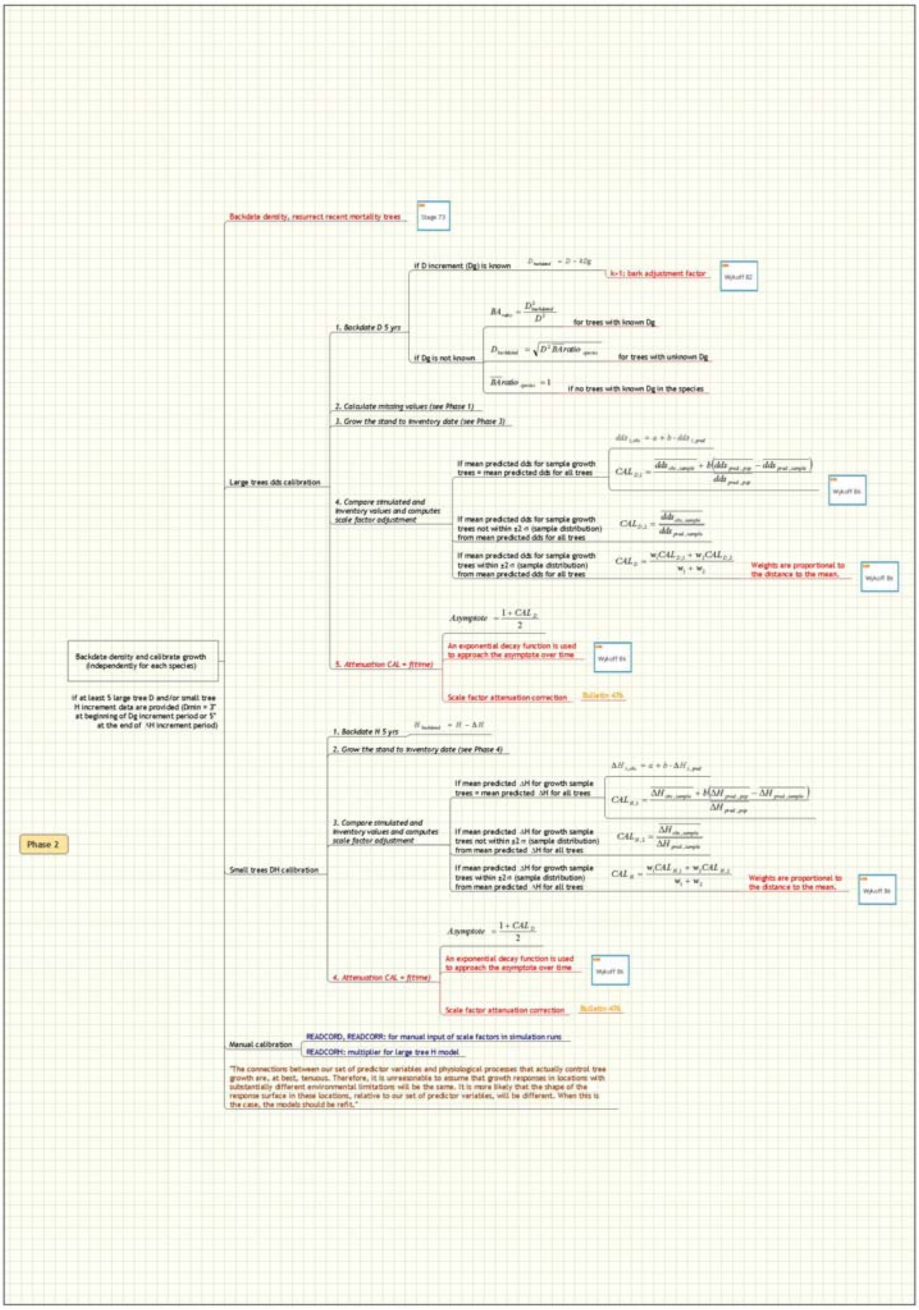
Development of a localized FVS version will provide many benefits to land managers at Fort Bragg. Most importantly, the project will satisfy the long-standing need for an accurate, unbiased growth model for the forest. Because of the large amount of data obtained from mature (70+ years old) longleaf pine stands, the models should perform well under stand conditions that provide suitable habitat for the endangered red-cockaded woodpecker. As the forest continues to mature, new growth data may be used to update submodel parameters and continuously fine-tune the local variant.

Working within the FVS framework takes advantage of many simulation and modeling capabilities that would be cost-prohibitive, if not impossible, to develop from scratch for a local landscape such as Fort Bragg. Integration of the Fort Bragg submodels into the existing Southern Variant provide the added advantage that future enhancements to the FVS framework, such as new keywords and pre- and post-processors, will be accessible to Fort Bragg managers without additional investment. As a result, it is likely that “buying in” to FVS today will continue to provide benefits into the foreseeable future.

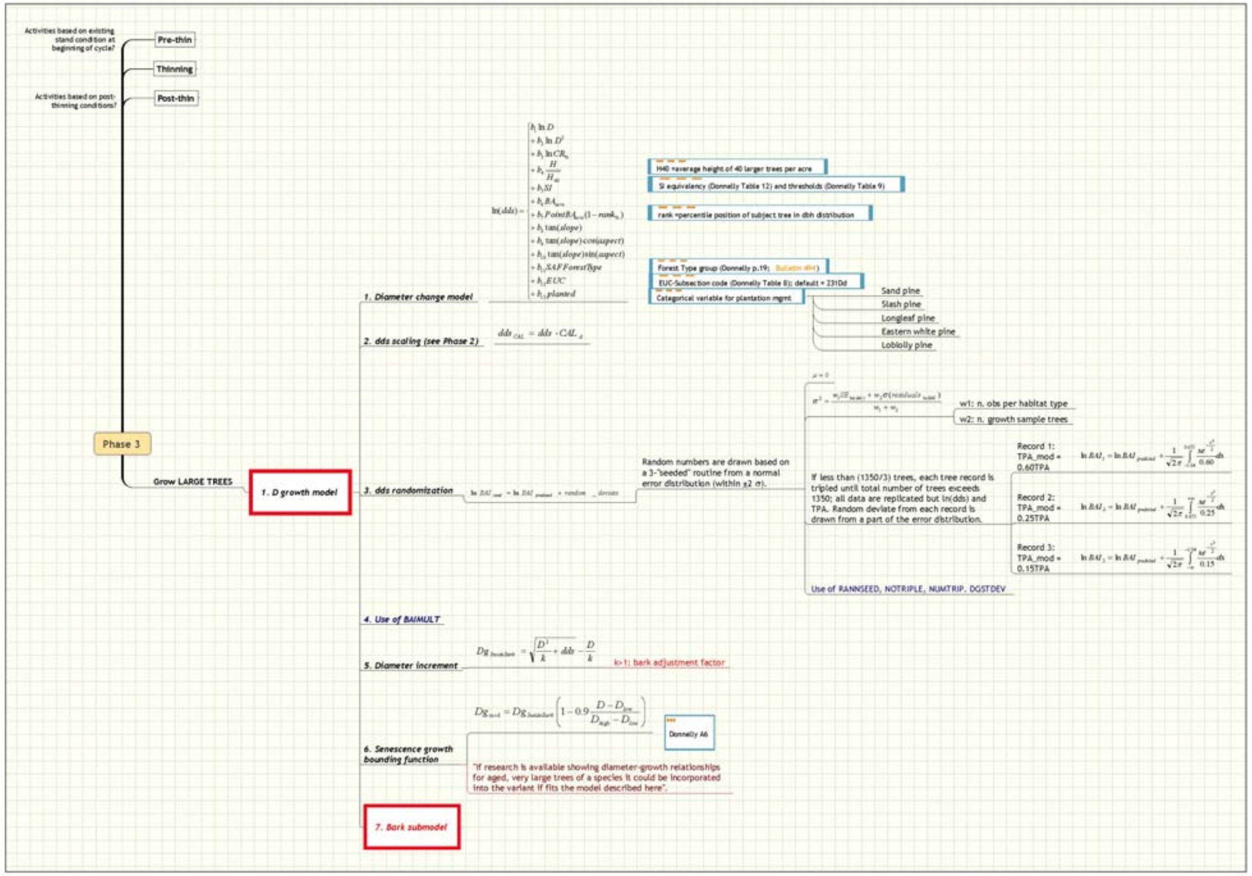
FVS has evolved continuously since the development of the original Prognosis model (Stage, 1973), and one mechanism by which this has occurred is user feedback and participation in model refinement. The process we used for development of the local variant can be repeated wherever adequate data are available.

Appendix 1


Phase 1
Pre-processors
Process .key and input stand/tree data
Compute initial stand characteristics (species-specific parameters)
Mapping of unrecognized species
Bulletin 558
Missing Tree height
If dbh >3"
$H = 4.5 + p_2 e^{-p_3 D^{p_4}}$
Donnelly A2
If dbh <3"
$H = 4.51 + \frac{4.5 + p_2 e^{-p_3 (3)^{p_4}}}{3 - DBW} D$
Donnelly A2
If at least 3 heights are provided; b0 calibrated according to data
$H = 4.5 + e^{b_0 - b_1 \left(\frac{1}{D+1}\right)}$
Donnelly A3
seedlings with a dbh of 0.1" or less will now get a dubbed height of 1 foot. Seedlings with a dbh greater than 0.1" will get a dubbed height of at least 4.5 feet. Users wanting initial seedling heights in the 1-4.5 foot range should provided them in the input data.
Bulletin 479
Missing Crown width
$CW = b_0 + b_1 D^{b_2}$
Donnelly A4
Parameters from open-grown or forest-grown trees?
The open-grown (==> CCF) and forest-grown (==> Canopy cover) crown width calculations for Regions 8 and 9 have been updated based on the references listed below.
Bulletin 581
Use of CWEQN
$CW = c_0 + c_1 D + c_2 D^{c_3}$
Bulletin 544
User-specified coefficients for trees having D < and > a specified threshold.
Use of FIXCW
Missing Crown ratio
1. Mean CR for each species
$MCR_{SDI\_class} = \frac{\sum_{i=1}^{n} (w_i CR\%_i)}{n}$
Wi: n. obs per CR% per relative SDI class
n: n. total observations
$MCR = f(SDI\_class)$
6 functions, the one with the highest R-squared for the species is retained
Donnelly A8
2. Weibull parameters
a, c= constant
$b = b_0 + b_1 MCR$
Donnelly A9
3. Individual CR assigned from Weibull cumulative distrib. according to tree BA percentile
Dixon 85
Use of CRNMULT



"The connections between our set of predictor variables and physiological processes that actually control tree growth are, at best, tenuous. Therefore, it is unreasonable to assume that growth responses in locations with substantially different environmental limitations will be the same. It is more likely that the shape of the response surface in these locations, relative to our set of predictor variables, will be different. When this is the case, the models should be refit."



Activities based on existing stand condition at beginning of cycle?

Pre-thin

Thinning

Activities based on post-thinning conditions?

Post-thin

Phase 3

Grow LARGE TREES

1. D growth model

1. Diameter change model

$$\ln(dds) = \begin{cases} b_1 \ln D \\ + b_2 \ln D^2 \\ + b_3 \ln CR_x \\ + b_4 \dfrac{H}{H_{40}} \\ + b_5 SI \\ + b_6 BA_{acre} \\ + b_7 PointBA_{acre}(1 - rank_x) \\ + b_8 \tan(slope) \\ + b_9 \tan(slope)\cos(aspect) \\ + b_{10} \tan(slope)\sin(aspect) \\ + b_{11} SAFForestType \\ + b_{12} EUC \\ + b_{13} planted \end{cases}$$

H40 =average height of 40 larger trees per acre

SI equivalency (Donnelly Table 12) and thresholds (Donnelly Table 9)

rank =percentile position of subject tree in dbh distribution

Forest Type group (Donnelly p.19; Bulletin 484)

EUC-Subsection code (Donnelly Table 8); default = 231Dd

Categorical variable for plantation mgmt

- Sand pine
- Slash pine
- Longleaf pine
- Eastern white pine
- Loblolly pine

2. dds scaling (see Phase 2)

$$dds_{CAL} = dds \cdot CAL_x$$

3. dds randomization

$$\ln BAI_{final} = \ln BAI_{predicted} + random\_deviate$$

Random numbers are drawn based on a 3-"seeded" routine from a normal error distribution (within ±2 σ).

$$\mu = 0$$

$$\sigma^2 = \frac{w_1 SE_{\ln(dds)} + w_2 \sigma(residuals_{\ln(dds)})}{w_1 + w_2}$$

w1: n. obs per habitat type

w2: n. growth sample trees

If less than (1350/3) trees, each tree record is tripled until total number of trees exceeds 1350; all data are replicated but ln(dds) and TPA. Random deviate from each record is drawn from a part of the error distribution.

Record 1: TPA_mod = 0.60TPA

$$\ln BAI_1 = \ln BAI_{predicted} + \frac{1}{\sqrt{2\pi}} \int_{-0.84}^{0.84} \frac{xe^{-\frac{x^2}{2}}}{0.60} dx$$

Record 2: TPA_mod = 0.25TPA

$$\ln BAI_2 = \ln BAI_{predicted} + \frac{1}{\sqrt{2\pi}} \int_{0.84}^{+\infty} \frac{xe^{-\frac{x^2}{2}}}{0.25} dx$$

Record 3: TPA_mod = 0.15TPA

$$\ln BAI_3 = \ln BAI_{predicted} + \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{-1.04} \frac{xe^{-\frac{x^2}{2}}}{0.15} dx$$

Use of RANNSEED, NOTRIPLE, NUMTRIP, DGSTDEV

4. Use of BAIMULT

5. Diameter increment

$$Dg_{insidebark} = \sqrt{\frac{D^2}{k} + dds} - \frac{D}{k}$$

k>1: bark adjustment factor

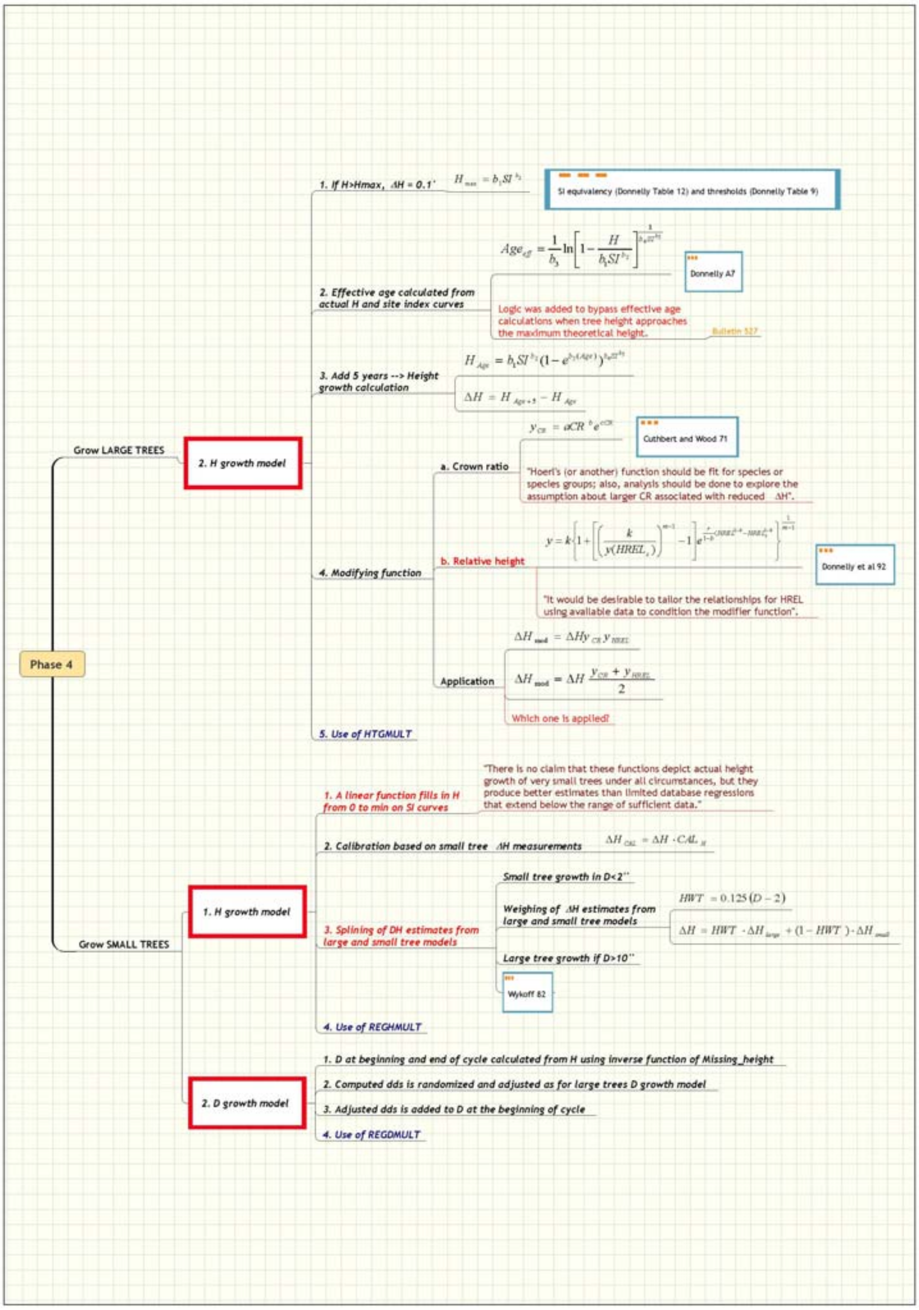
6. Senescence growth bounding function

$$Dg_{mod} = Dg_{insidebark}\left(1 - 0.9\frac{D - D_{low}}{D_{high} - D_{low}}\right)$$

Donnelly A6

"If research is available showing diameter-growth relationships for aged, very large trees of a species it could be incorporated into the variant if fits the model described here".

7. Bark submodel



Logic was added to bypass effective age calculations when tree height approaches the maximum theoretical height.

"Hoerl's (or another) function should be fit for species or species groups; also, analysis should be done to explore the assumption about larger CR associated with reduced ΔH".

"It would be desirable to tailor the relationships for HREL using available data to condition the modifier function".

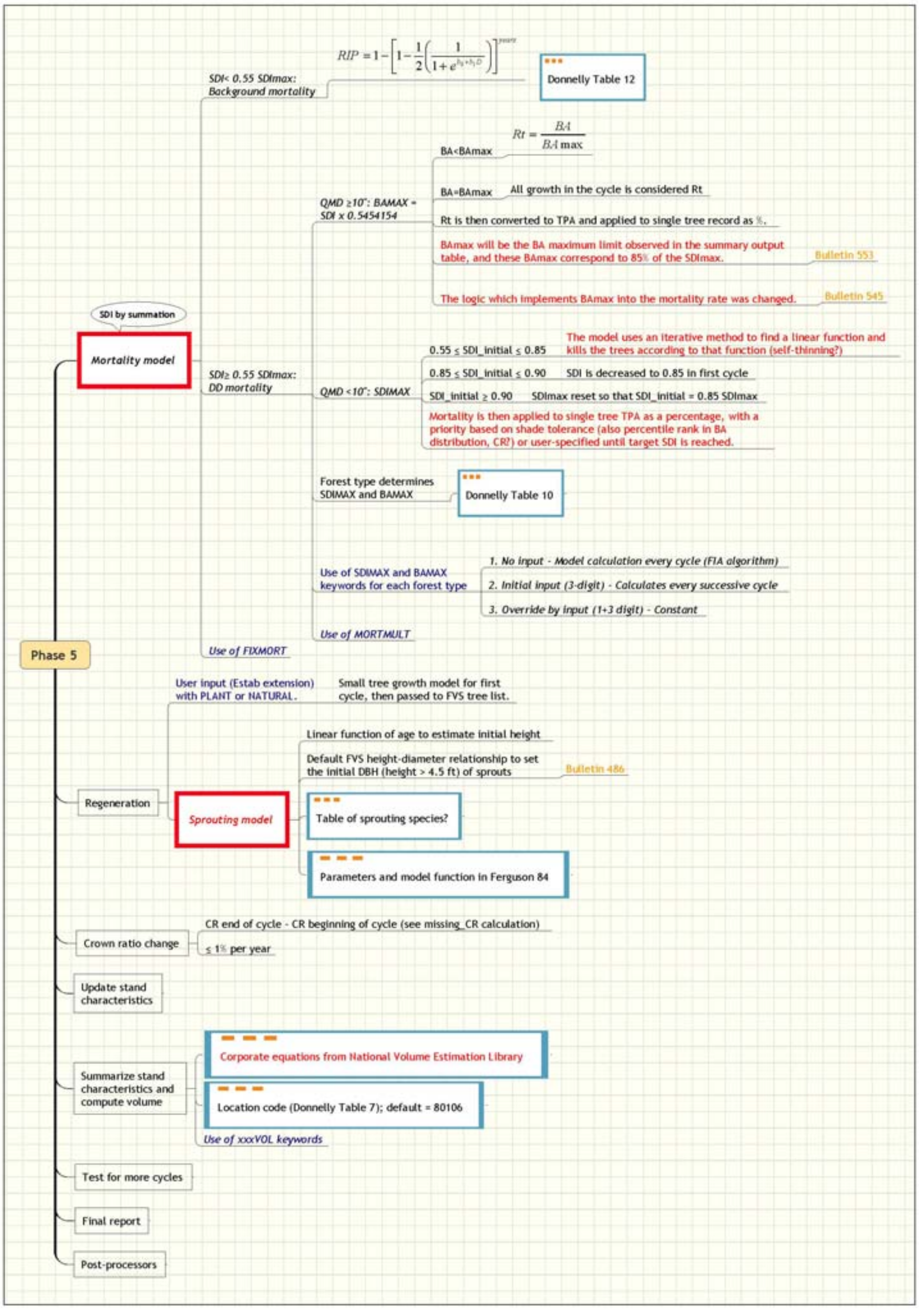
Which one is applied?

"There is no claim that these functions depict actual height growth of very small trees under all circumstances, but they produce better estimates than limited database regressions that extend below the range of sufficient data."

1. D at beginning and end of cycle calculated from H using inverse function of Missing_height

2. Computed dds is randomized and adjusted as for large trees D growth model

3. Adjusted dds is added to D at the beginning of cycle


Phase 5
SDI by summation
Mortality model
SDI< 0.55 SDImax: Background mortality
$RIP = 1 - \left[1 - \frac{1}{2}\left(\frac{1}{1+e^{b_0+b_1 D}}\right)\right]^{years}$
Donnelly Table 12
SDI≥ 0.55 SDImax: DD mortality
QMD ≥10": BAMAX = SDI x 0.5454154
BA<BAmax
$Rt = \frac{BA}{BA\max}$
BA=BAmax
All growth in the cycle is considered Rt
Rt is then converted to TPA and applied to single tree record as %.
BAmax will be the BA maximum limit observed in the summary output table, and these BAmax correspond to 85% of the SDImax.
Bulletin 553
The logic which implements BAmax into the mortality rate was changed.
Bulletin 545
QMD <10": SDIMAX
0.55 ≤ SDI_initial ≤ 0.85
The model uses an iterative method to find a linear function and kills the trees according to that function (self-thinning?)
0.85 ≤ SDI_initial ≤ 0.90
SDI is decreased to 0.85 in first cycle
SDI_initial ≥ 0.90
SDImax reset so that SDI_initial = 0.85 SDImax
Mortality is then applied to single tree TPA as a percentage, with a priority based on shade tolerance (also percentile rank in BA distribution, CR?) or user-specified until target SDI is reached.
Forest type determines SDIMAX and BAMAX
Donnelly Table 10
Use of SDIMAX and BAMAX keywords for each forest type
1. No input - Model calculation every cycle (FIA algorithm)
2. Initial input (3-digit) - Calculates every successive cycle
3. Override by input (1+3 digit) - Constant
Use of MORTMULT
Use of FIXMORT
Regeneration
User input (Estab extension) with PLANT or NATURAL.
Small tree growth model for first cycle, then passed to FVS tree list.
Sprouting model
Linear function of age to estimate initial height
Default FVS height-diameter relationship to set the initial DBH (height > 4.5 ft) of sprouts
Bulletin 486
Table of sprouting species?
Parameters and model function in Ferguson 84
Crown ratio change
CR end of cycle - CR beginning of cycle (see missing_CR calculation)
≤ 1% per year
Update stand characteristics
Summarize stand characteristics and compute volume
Corporate equations from National Volume Estimation Library
Location code (Donnelly Table 7); default = 80106
Use of xxxVOL keywords
Test for more cycles
Final report
Post-processors

Chapter V: Synthesis and conclusion

The main objective of this thesis was to provide an answer to the need for a deeper knowledge of stand dynamics in Scots pine forests of the southern Alps. Recent changes in land use management, and climate shifts determining alterations in biotic and abiotic disturbance regimes, raise concerns about the continuity of the services supplied by the pine forests. Consequently, prospects for the multifunctional exploitation of such resource must be supported by a thorough understanding of ongoing trends in the evolution of the geographical distribution of the species and of structure and composition of its stands.

We identified competitive dynamics as the key factor shaping stand development. The analysis of competition and mortality in Scots pine stands was carried out with a multiscalar perspective. On one hand, we showed how competitive dynamics strongly affect tree growth and survival. A tree-scale approach evidenced the leading role of competition for light, which was expected due to the early-seral character of the species under study, but also the differences in competition intensity and its spatial extent determined by land use history and current successional pathways. We proposed a conceptual model of the interactions between resource availability, competition and tree response, by means of comparing a pure, even-aged stand in stem-exclusion phase (Oliver and Larson, 1996) with a more complex stand characterized by a longer history of human exploitment and by more advanced successional traits.

On the other hand, we used a combination of methods to explore the emergent properties of competition at the higher hierarchical stage (*sensu* O'Neill et al., 1986; see also Prentice and Leemans, 1990), namely the stand level. When mortality takes the place of plastic adaptation as a tree's response to neighbor-mediated resource exploitation, long-term consequences are triggered in the stand's horizontal and vertical structure, species composition and interactions with exogenous regulatory factors. We found relative density to be a reliable index of a stand's competitive status; the past history of competition was assessed by means of complementary analysis of living and dead tree's spatial pattern. To this regard, we provided field-based evidence to Watt's (1947) theory of pattern and process, i.e., the hypothesis that properties of plant communities such as species composition, population structure, canopy profiles, successional paths and self-thinning trajectories are predictable from the lower-level mechanisms by which individual plants affect and respond to their immediate environment (Prentice and Leemans, 1990).

Furthermore, thanks to the integration of independent sources of analysis in reconstructing stand establishment and past history, we could gain an insight in the ecological dynamics triggered by alterations in the anthropogenic impact on the forest. The pattern of land abandonment and forest expansion that has been highlighted by recent studies (Garbarino et al., 2006) was paired to a process-centered understanding of Scots pine's establishment mode and subsequent stand development in the most important cover types of this species in the study area. To this regard, the role of past anthropic impact proved fundamental in shaping current stand structure and composition. We confirmed that Scots pine, due to his autoecological traits and current geographical distribution, responds with great sensitivity to land use changes, both on the stand- and on the landscape scale.

The interactions between tree- and stand-level dynamics showed their importance in our modeling application. Simulation of future growth and yield on a mid-term temporal scale (10 to 100 years) is a useful tool for managing forest resources and forecast stand conditions and functions, as shown by the red-cockaded woodpecker – Longleaf pine ecosystem simulation case. In most cases, existing models cannot be effortlessly applied to species or geographical ranges different than the ones they were designed for. US Forest Service's Forest Vegetation Simulator proved its flexibility in being calibrated to local data, in order to better reflect site-specific growing conditions. Moreover, there is a trend in forest ecology research aiming at joining forest growth simulators to models for disturbance factors interacting with the stability of future stands, such as in the case of rockfall or avalanche modeling (Botkin et al., 1972; Shugart, 1984; Hasenauer et al., 2000; Bugmann, 2001; Courbaud et al., 2001; Lexer and Hönninger, 2001; Rammig et al., 2006). We foresee such a modeling environment to be a valuable tool for forest management also in the Alpine setting, provided that suitable data be available for model re-calibration and additional research be carried out to interpret the form and influence of the main growth relationships (Monserud and Sterba, 1996). Deviations of actual growth from the model can be tested against other tree condition variables or changing environmental conditions or stresses (Steyrer, 1996; Solberg and Tveite, 2000; Solberg, 2004; Spitzbart and Sterba, 2004; Dobbertin, 2005).

The inventory planning and validation tasks detailed in Chapter IV offered the opportunity to evaluate the amount, geographical extent and precision needed for a model-oriented sampling of forest resources. The Second National Italian Forest Inventory (INFC, 2005) is currently under development. Should data availability be guaranteed, it is likely that its sampling design and field protocol specifications (INFC, 2004, 2006) will allow gathering tree and stand data measured on a large spatial extent and accurate enough for model-oriented statistical treatment and summarization. If necessary, such data could be integrated by the existing Regional Forest Inventories, even though these are characterized by significant differences in the definition of the sampling unit and measured variables (Tosi and Monteccone, 2004). If supported by adequate field and documentary evidence, the methods applied in the present research may be applied to the modeling and prediction of stand dynamics in other key forest types of the Alpine ecoregion.

In the course of the present research, a network of permanent sample plots has been established in alpine Scots pine forests representative of different ecosites and land use history. The establishment of such a permanent monitoring network will prove its utility when repeated measurements be conducted in the upcoming future. While inventory data may be sufficient for modeling purposes, intensive periodic monitoring of tree and stand conditions is crucial for assessing current and future vitality of individuals and the evolution of their response to stress in time (e.g., Dobbertin, 2005). As an example, we cite the EU-INTERREG reaserch project currently underway, aimed at understanding the causes of the dieback wave which has been occurring in Alpine Scots pine stands since the last ten years. Within this scheme, the indices tested herein have been used in analyzing the role of stand density and neighbors influence on tree vitality as assessed by foliage density measurements [Figure 58].

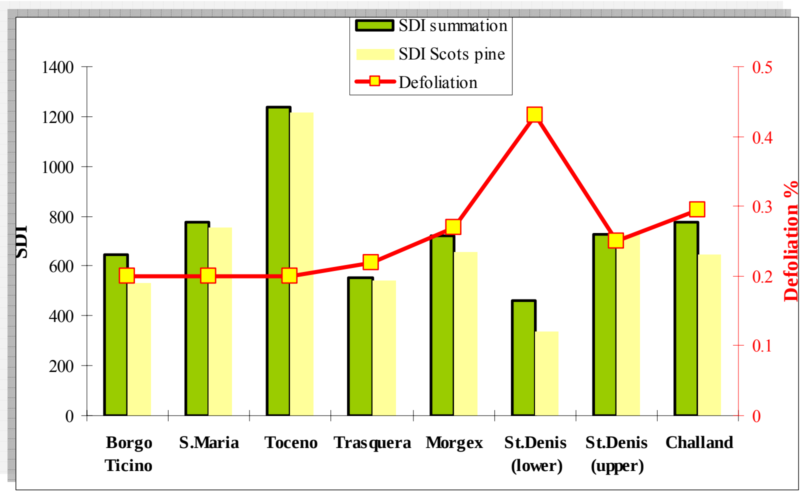


Figure 58 – Stand-level data from the present study are combined with information on forest health condition, i.e., mean crown transparency data from the 2006 assessment (Dobbertin, unpublished data). The absence of correlation between stand density and tree health must direct research to other causes for the inquired process.

Last, Chapter II of this dissertation detailed the design and testing of a region-wide modeling tool for stand dynamics. The inner structure of Density Management Diagrams, based on general mortality and biometric functions, allowed us to link the assessment of current and future stand structure to the projection of the impact of disturbances (including silvicultural operations). This tool represents the ultimate goal of the ecological analysis presented herein, in that it incorporates the emergent properties of endogenous stand dynamics acting on smaller scales, combined with the opportunity to address the long-term effects of exogenous regulatory factors, even the ones that may result from altered background climate conditions (e.g., Schumacher et al., 2004). Moreover, achievement of different forest functions by means of silvicultural management strategies may be compared and effectively modeled. For this reasons, we believe DMDs to represent an invaluable instrument for planning sustainable management strategies.

It should finally be noted that the modeling tools presented in this thesis are best applied on a short- to mid- spatiotemporal extent, i.e., for the forecasting of tree growth and stand structure on a period of one to few hundreds years (Crookston and Dixon, 2005). Climate change-related issues may certainly alter growth and survival dynamics of the system under study, since ecological processes may change with changing conditions (Penuelas and Filella, 2001; Theurillat and Guisan, 2001; Walther, 2004). An estimation of forest response to climate change has to deal with many problems (Hanninen, 1995; Loehle and LeBlanc, 1996; Hanson and Weltzin, 2000), particularly when studying managed forests. Modeling tools suited for this kind of analysis and based upon larger spatio-temporal scales have already been developed (e.g., Weber, 2005; Wehrli et al., 2005). Nonetheless, the insights gained into the functioning of the pine forest system in the current environmental conditions, its regulatory factors and the tools tested for predicting its future status provided the groundwork on which to project prospective scenarios of change.

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