GROWTH PATTERNS, COMPETITION AND COEXISTENCE IN GAP-PHASE REGENERATION UNDER CLOSE-TO-NATURE SILVICULTURE

Marco Dekker

Growth patterns, competition and coexistence in gap-phase regeneration under close-to-nature silviculture

Groeipatronen, concurrentie en coexistentie in natuurlijke verjonging in kronendakgaten onder natuurvolgend bosbeheer

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“Long is the way and hard, that out of darkness leads up to light”

(Adapted from Milton, Paradise Lost)

CONTENTS

ABSTRACT

The dominant European forest policy objective is to create multifunctional, mixed-species and uneven-aged forests. This objective includes the nature-oriented conversion of monospecific plantations. To reach this objective, close-to-nature silviculture is applied. This generally entails natural regeneration in canopy gaps. In the Netherlands, experience with gap-phase regeneration is limited, making it difficult to asses the effect of close-to-nature management on forest development. In this thesis, this problem is addressed by investigating species coexistence between the four dominant species that occur in naturally regenerated canopy gaps in Douglas fir forest in the Netherlands. These species are Silver birch (*Betula pendula* Roth.), Japanese larch (*Larix kaempferi* Carr.), Scots pine (*Pinus sylvestris* L.) and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco).

During gap-phase regeneration, saplings undergo self-thinning. This affects species composition of the regeneration unit. Important factors in self-thinning are species-specific morphological growth patterns, emergent stand characteristics, the effect of stand characteristics on competitive relationships, and the effect of light availability on growth and mortality. Growth patterns differed between species and resulted in differences in the achieved height per unit biomass. Differences in mass-based heights subsequently caused a vertical stratification in the regeneration unit which, in turn, affected the interspecific competition for light. However, results demonstrated a competitive response rather than a competitive effect. Surrounding saplings formed a functionally equivalent neighborhood, and target individuals responded mainly to their position in the canopy.

Canopy position affected the radial growth of saplings. Mortality probabilities depended on radial growth, but did not differ between species despite a wide range in light demand. Scots pine did not show a relation between growth and mortality, even though it is highly responsive to light. Under continued autogenic development, a low-density top stratum of Silver birch and Japanese larch will develop, overtopping a declining number of Scots pine and a large number of increasingly dominant Douglas fir. This implies that Scots pine will be outcompeted by the other species, and Douglas fir will gain dominance in the future. Forest conversion by natural regeneration will therefore not lead to the desired mixed-species composition, but stands will eventually revert back to Douglas fir forest. Maintaining a diverse forest thus means the need for interventions in the early developmental stage.

CHAPTER 1

Introduction

Close-to-nature silviculture

In the Netherlands close-to-nature silviculture (Gayer, 1898) is applied to transform monospecific plantations into uneven-aged mixed-species forests. On a bigger scale, the principles of close-to-nature silviculture underlie many forest policies in Europe. Policies that generally aim to create more natural forests. In fact, current views on sustainable forest management incorporate many elements of close-to-nature silviculture, for example to follow and mimic natural ecosystem dynamics.

The current application of close-to-nature management serves the purpose of making the Dutch forests more diverse, increasingly natural, and better adapted to the needs of society. There is, however, no long-term experience in applying such management in the Netherlands, and it is unknown how forests develop under it.

It appears therefore that the methods and goals are set, but that their match remains uncertain. A better understanding of this match lies in bridging the gap between methods and goals, that is to say, to connect the short-term interventions with long-term objectives. In the transformation of monospecific plantations, particularly the effect of close-to-nature management on species composition is important. A better understanding of this effect would allow the evaluation of what in general has become an important approach in forest management in the Netherlands: close-to-nature silviculture.

Historical background

Since the Middle-ages increasing population pressure, war and lack of regulation led to large-scale deforestation in central and north-western Europe. Forests were often used as communal grounds and were largely overexploited. By the end of the eighteenth century, next to deforested areas, many degraded forests were left. The fear of wood shortages forced people to start actively managing the forest estate and restoration and reforestation started (Gayer, 1898).

As the forest had always been important for wood and non-wood products, people adapted the existing forests to their needs by maximising their utilitarian value. The usual practice was to harvest the older and bigger trees for wood, and cut the younger and smaller trees for cattle fodder (also in coppicing systems). As mainly the trees in the middle size classes were left, slowly a single layer forest was created (Van Schermbeek and Gayer, 1898). Some species were more suited to this type of management, or were in greater demand, and/or performed better on degraded soils, and in the end monocultures were created. The focus was mainly on less demanding or highly valued species such as *Pinus* spp and *Quercus* spp. These species were often planted (Van Schermbeek and Gayer, 1898).

In the beginning of the 19th century technological developments provided the opportunity to afforest larger areas. Together with a changing demand in wood products (less firewood and more building material), as well as a

rational and schematical approach to forest management, slowly a forest management system was created that worked with even-aged monocultures. These monocultures were planted and clearcut after a specified rotation age was reached (Huss, 1990). Such monocultures became wide-spread in Europe but had a number of problems associated with them like insect attacks, snowbreak, windthrow, and fire outbreaks (Van Schermbeek and Gayer, 1898).
As a reaction to the large-scale implementation of even-aged monocultures, and as a response to the problems associated with them, Gayer (1898) advocated the use of uneven-aged mixed forests and for the first time the term ‘close to nature’ was used (Huss, 1990). These mixed forests were claimed to be more resistant, better adapted to the needs of society and the demand for a diversity of wood products, and more sustainable (Gayer, 1898). In general Gayer advocated a dismissal of the even-aged and schematic clearcut system and the rational approach to forest management associated with it, and instead placed the focus on long-term regeneration processes, a group selection system and a ‘back to nature’ approach (Huss, 1990). This way of thinking led to a view in which the forest was regarded as a complex organism that needs to be healthy in all aspects. This finally developed into the *Dauerwald* movement (Möller, 1922), in which there was no place for a schematically ordered and schematically exploited forest. Rather than following a technical blueprint, the *Dauerwald* movement took the natural conditions in the forest as a starting point for management. The forest was thus primarily regarded as a biological entity, but wood production always remained an important function of the forest (Hehn, 1990). Even though the forest was seen as an ecosystem, at this time natural values in themselves (e.g. biodiversity) were not an explicit goal and no reference was made to the specific maintenance of species, habitats etc. A good production forest was seen as a mixed, uneven-aged forest in which (group-) selection harvest is applied, composed of species that are suited to the site conditions, and that shows good annual increment.

What is important to recognize in the historical development of close-to-nature silviculture as outlined above, is that it is based in an organic view on forests which opposed the mainstream rational and technical approach to forest management. This underlines the philosophical starting point of close-to-nature silviculture (an organic instead of a technical-scientific worldview). It also suggests that the distinction between close-to-nature silviculture and even-aged management is not a simple dichotomy between two objectively and well defined systems, but that there is a non-rational and subjective-emotional aspect in what is considered close to nature, and close-to-nature management. Hehn (1990) summarises the idealistic foundation of close-to-nature silviculture in three principles, which, at the same time, demonstrate that they cannot give rise to a clearly defined forest management system, strictly separated from other management systems:

1. Protect, maintain and utilise the forest as an entire ecosystem, both above and below ground
2. Dismiss all aspects related to the clearcut system, make decisions at the single tree level
3. Try to understand the forest by observing the natural variation in the forest, regard this variation as a fundamental property of the entire ecosystem, and incorporate it into forest management

Politcal embedding

Contrary to monospecific forest management, close-to-nature silviculture was never massively taken up after it was conceived in the first half of the twentieth century. By the end of the twentieth century the combined European forests had increased in area by as much as 10%, in total covering about 33% of Europe's land area. This was however mainly the result of afforestation with coniferous species, and the European forests were increasingly homogenous and artificial. A total of six species in four genera (*Pinus*, *Picea*, *Fagus* and *Quercus*) made up two-third of all trees (Stanners and Bourdeau, 1995).

In addressing these developments, current European forest policy reflects global policy processes. On a global level there had been a rising attention for sustainable development and the conservation of biodiversity. This attention culminated in the United Nations Conference on Environment and Development in 1992. Some key European policies that implement this global policy framework are the MCPFE Helsinky Resolutions (MCPFE, 2000), the Pan-European Biological and Landscape Diversity Strategy (CoE, 1995), the Community Forestry Strategy and the Community Biodiversity Strategy (EC, 1998a, 1998b). These policy documents present guidelines in areas like wood production, the conservation of biodiversity, recreational values and landscape amenity. They furthermore emphasise a sustainable and multi-functional forestry that incorporates all societal demands on forests. These guidelines generally share the organic ecosystem-view that underlies close-to-nature silviculture. This is illustrated by guidelines to use silvicultural practices emulating nature and to maintain natural structures and processes (MCPFE, 2000), guidelines to refrain from intensively managed monocultures and to maintain ecological integrity (CoE, 1995), and guidelines to focus on natural regeneration and to maintain health, vitality and resistance of the forest (EC, 1998a).

These examples point out that the objectives and methods as proposed in close-to-nature silviculture are for a large part embedded in contemporary European forest policies. Close-to-nature silviculture is not explicitly advanced as a preferred management system, but it does become clear that there is a strong societal and political interest in natural forms of forest management, which fits closely together with close-to-nature silviculture. These natural forms of forest management are mainly characterized by an emotional content that is expressed in generic terms, i.e. in a framework of desirable concepts like naturalness, sustainability and multi-functionality. The sought-after (natural) forest management, however, is not captured in definitions and delineations, or in particular silvicultural systems. It is therefore important to realize that what is conveyed in forest policies is mainly a mindset, and not a technical directive.

Contemporary application

Schütz (1999b; 1999c) states that close-to-nature silviculture aims to create a well structured, mixed-species forest of natural species composition and of good economic performance. Such management is thought to approach natural ecosystem dynamics and therefore is more stable and cost-effective to manage. Yet, it should be realized that a 'close-to-nature forest' remains a production forest that still can be intensively managed, as pointed out by Maguire (2005). An uneven-aged multi-species forest therefore does not by definition equal low-intensity management. Overall, close-to-nature silviculture aims to maintain a forest's potential to fulfil ecological, economical and societal functions (Eder, 1997).

A management approach from North-America that is similarly based in natural dynamics and the incorporation of the socio-economic context into management is Ecosystem Management (Christensen et al., 1996). Ecosystem Management is a relatively recent approach which only gained momentum since the 1980s (see Grumbine, 1994). It is described in abstract terms like adaptive management and sustainability. Fundamental characteristics of Ecosystem Management, according to Christensen et al. (1996), are:

1. Uphold long-term sustainability as a core value
2. Have clear operational goals
3. Have a sound understanding of ecosystem components and functioning
4. Appreciate the complexity and interconnectedness of ecosystems
5. Recognize the dynamic character of ecosystems
6. Pay attention to context, and spatial and temporal scales
7. Acknowledge humans as ecosystem components
8. Commit to adaptive management

Contemporary close-to-nature silviculture on the other hand is a further development of the *Dauerwald* movement which started with Gayer in the late nineteenth century. It is practical and technical, described in terms of stand characteristics and management activities (Hehn, 1990; Otto, 1993a; Hockenjos, 1999). Hockenjos (1999) states the specific objectives of close-to-nature silviculture, which can be seen as translating the three underlying principles mentioned earlier to a practical level. They are to:

1. Achieve forest stability
2. Maintain a natural species composition
3. Create mixed-species, uneven-aged forests
4. Focus on natural regeneration without clearcutting
5. Do not counteract natural developments in forest operations
6. Apply an appropriate hunting policy
7. Apply biological measures against pests and pathogens
8. Apply low-impact harvesting techniques

Similar objectives can be found in different wordings with many authors (e.g. Hehn, 1990; Huss, 1990; Otto, 1993b; Eder, 1997).

Different as Ecosystem Management and close-to-nature silviculture may be (conceptual versus practical), in forest management they are merged into one combined approach that is sometimes referred to as 'back to nature'. This merger can be recognized in the overall management objectives on the one hand, and the proposed management activities and forest characteristics on the other (Bengtsson et al., 2000; Farrell et al., 2000; Führer, 2000; Piussi and Farrell, 2000; Gamborg and Larsen, 2003; Spiecker, 2003; Dorren, 2004). The following extract, adapted from the before-mentioned papers, outlines this merger:

> Forest management must meet many demands placed on it, ranging from wood production and nature conservation to social and cultural functions. It has to meet these ecological, economical and societal objectives while coping with long-term ecosystem dynamics and short-term disturbances. To be sustainable, forest management must therefore focus on persistence and stability of the forest, which can be done by applying methods aimed at preserving the environment and biodiversity while maintaining timber yields. Conditions promoting ecological stability are a diverse species composition, sufficient natural regeneration and an optimal forest structure. In practice this means imitating natural disturbances and dynamics through small-scale management aimed at heterogeneity, e.g. by harvesting the forest on a small scale, retaining patches of unmanaged old-growth forest, and allowing old trees and dead wood to develop. This will yield the niches that allow biological diversity to develop, for example hollow trees, mosaics of open and dense areas, and large snags. In making these management decisions, it is important to always follow natural forest developments. Working against natural dynamics would lead to a breakdown of the forest and the management system in the end. Both ecosystem dynamics and social dynamics must be incorporated into management, and this makes adaptive forest management a necessity. This means that forest management changes along with environmental and societal changes.

From this outline it can be seen that Ecosystem Management (as applied in forest management) has merged with close-to-nature silviculture (see also Pommerening and Murphy, 2004). This merger connects the broader objectives of Ecosystem Management with technical aspects and stand-level detail on management activities and forest characteristics of close-to-nature silviculture. This is also referred to as an Ecosystem Approach (UNEP, 2000). What is relevant in this connection between overall objectives and practical activities is that it assumes a direct relationship between them. For example, that small-scale management applying natural regeneration leads to mixed, stable and productive forests. Whether this is the case is by no means certain.

Close-to-nature silviculture as a social construct

The current attention for natural forest management means that it is mainly an umbrella term for all approaches dealing with structure, composition and forest dynamics (Gamborg and Larsen, 2003). A number of such forest management concepts exists side by side, with no specific hierarchy between them, and all have their own origin and peculiarities. These concepts are *inter alia* continuous cover forestry, forest management based on natural processes and nature-oriented silviculture, which Pommerening and Murphy (2004) consider to be semi-synonymous. Trying to find generality in such descriptors without attention to context-dependent details will only lead to confusion and the use of them as hollow buzzwords (Goldstein, 1998). As with sustainability itself, producing personal definitions does not resolve the vagueness and lack of solid meaning that is to some level inherent to these concepts (Newton and Freyfogle, 2005). In essence, however, all these approaches aim to create natural, mixed, uneven-aged forests in which products and services are produced, that are valued in society, and in which biodiversity is conserved. They do so by mimicking natural processes, for example group harvesting that imitates gap dynamics. This description will be used as an operational definition of close-to-nature silviculture in this thesis (also see Definitions section later on).

But what is close to nature, what is natural, which reference image does this refer to? In answering these questions one has to consider the aspect of species (e.g. presence of indigenous or exotic species, what flora and fauna would naturally occur, in which proportions), the aspect of forest structure (e.g. age structure, horizontal and vertical forest structure, mosaics of developmental stages), and the aspect of ecological processes (e.g. frequency and intensity of large and small disturbances, level of mortality and regeneration, succession, wild life levels). All these matters have to be dealt with in close-to-nature management, and this inescapably entails some subjectivity.

Two extreme positions that define an axis of naturalness ranging from anthropogenic to natural forests, are respectively (Londo, 1991):

1. A fully anthropogenic forest that is uniform in age structure (at the stand level), and in which species composition is very much influenced by human activities
2. A completely natural forest in which the influence of human activities is small to non-existent. These forests usually have a varied species composition and a differential age structure

The question that however still remains is what characteristics make a natural forest. This has a primarily ethical-emotional content and cannot be captured in definitions. It is a subjective interpretation of the concepts of nature and naturalness (Schütz, 1999b). The image of nature in Europe that emerged from the previous centuries is a romantic image of a wild place with many plant and animal species and lots of structure. However, when ecosystems are left to themselves they can develop into structurally and species poor environments, and that does not coincide with our image of nature (Van der Windt, 1995). This is linked to a dominant holistic view on nature in which ecosystems comprise sets of species in balance with their environment, and where missing species indicate disturbed ecosystems that can or should be returned to their original state (De Jong, 2002). This likely is the reason why, currently, management interventions are generally aimed at a controlled development towards a predefined goal, rather than letting natural processes simply take their course (Van der Werf, 1991; Al et al., 1995; Stortelder et al., 1999; Bal, 2001).

An exact reference image for this predefined goal however, i.e. a completely natural forest, cannot be determined for lack of data and attempts are often controversial (e.g. Vera, 1997). A reference image also depends on which historical period in human population development is to be used as a reference. Additionally, one would also have to assess the spontaneous, natural developments that would have occurred without human influence since that reference period. Any fixed reference image is therefore inevitably illusive, and depends on both facts as well as interpretations (Al et al., 1995; De Jong, 2002).

An often used reference image for naturalness is a concept from plant sociology: the Potential Natural Vegetation (PNV). This is the climax-vegetation that (hypothetically) would develop if all human influence would stop. It is determined based on reconstructions using pollen analysis. The question how to determine which species other than trees or herbs, and which structures and processes are part of the PNV, is answered by looking at remaining ‘primary’ forest remnants in Europe, like *Bialowieza* in Poland and the *Neuenburger Urwald* in Germany (Van der Werf, 1991; Van der Windt, 1995). To what level these forests provide a relevant comparison however is unclear as these forests are also subject to long-term anthropogenic influence, and subjective notions on what is natural are never really escaped.

Furthermore, any development in actual stands is highly context-dependent and may greatly divert from the postulated PNV.

In short, humans have shaped Europe’s forests for thousands of years (Kirby and Watkins, 1998) and continue to do so based on contemporary demands like biodiversity and recreational values (MCPFE, 2000; UNFCBD, 2004). Society now places a high value on such values, which has created a decrease in importance of the forests’ commodity function (Spiecker, 2003). The dominant approach in forest management is that we should focus on using natural, autogenic processes in forest management (Bengtsson et al., 2000), even though this cannot be objectively or scientifically delineated. Close-to-nature silviculture therefore is characterized by two important dimensions: an emotional value-driven socio-political dimension, as well as a technical science-driven ecological dimension. Consequently, close-to-nature silviculture cannot be seen as simply conveying objective scientific truths on how to manage forests sustainably.

The re-orientation on close-to-nature silviculture in the Netherlands: transformation management of even-aged monocultures

Many elements of close-to-nature silviculture are found in the current view on sustainable forest management, which is a leading management paradigm. Sustainable forest management is filled in with an ecosystem-stewardship role for forest managers (Kennedy et al., 2001) and accordingly, increased emphasis is placed on close-to-nature management rather than on rationalistic wood production (Spiecker, 2003). Irrespective of the particular silvicultural system that is applied, sustainable forest management generally involves leaving a continuous canopy cover (i.e. no large-scale clearcutting), and applying natural regeneration. The emphasis on a sustainable forest management, by means of close-to-nature silviculture, has therefore lead to a focus on natural regeneration in canopy gaps.

In the past, many coniferous plantations were established in Europe. The conversion of these monospecific and artificial stands into mixed-species uneven-aged forests is now one of the current challenges in silviculture (Farrell et al., 2000; Zerbe, 2002). In the Netherlands, even-aged forests make up 83 percent of the total forest area (period 2001-2005). This is a high share but it already has been brought down from 99 percent in the 1980s. In this same period uneven-aged forests have increased from 0.2 to 17 percent (LNV, 2007). Subsidies are in place that encourage such transformation of monocultures into more natural forests. They do so by rewarding the presence of indigenous trees, large-sized trees and dead wood, and by discouraging non-indigenous monocultures (e.g. see Groenloket, 2007).

The attention in the Netherlands for natural forests and natural regeneration stems mainly from the early 1970s when two severe storms created extensive windthrows in the Dutch forests. Natural regeneration massively sprung up after these storms, inspiring forest managers and conservationists alike. Up to that point mainly even-aged clearcut systems were in use, but after these storms, and led by vegetation scientist Westhoff (1976) and *Kritisch Bosbeheer* (Kleijn and Cosijn, 1980), attention grew for creating natural forests out of the artificial plantations (defining 'natural' was rather problematic however, as explained before).

Natural regeneration plays a central role in this objective of transforming artificial plantations. To transform the legacy of even-aged monocultures, canopy gaps are often created in order to initiate natural regeneration. Gap-phase regeneration allows different species to establish in a spatially and temporally irregular pattern. This is thought to give rise to uneven-aged mixed-species forests in the long term. Natural regeneration not only plays an important role in adapting to climate change, for example by establishing the most adapted species composition through autogenic forest development (Brown, 1996; Lindner, 2000; Spittlehouse and Stewart, 2003). But using such natural processes might also lower costs of management. Not just by naturally regenerating, but also by using self-thinning and self-pruning (Schütz, 1999a).

In the Netherlands, the particular approach to natural forest management is Integrated Forest Management (*Geïntegreerd bosbeheer*), a Dutch form of close-to-nature silviculture. This approach is endorsed in Dutch forest policy (LNV, 2000), and aims at integrating nature conservation, recreational values and wood production. It is also applied in the transformation of even-aged monocultures to mixed uneven-aged forests (Van der Jagt et al., 2000). Transformation management will particularly occur in monospecific even-aged stands in order to meet the multi-functionality principle that underlies Integrated Forest Management.

Under Integrated Forest Management first the productive potential and the recreational and conservational values of a forest stand are evaluated. A choice is then made whether to place an emphasis on any of these three forest functions, but despite any emphasis all three functions have to be substantially present in the forest. After this evaluation, management interventions will take place where stands do not meet evaluation criteria (regarding species mixture, growth level, the presence of dead wood, structural variation, good quality regeneration, the presence of potential crop trees and aesthetic trees). This can lead to relatively rigorous interventions (again at the stand level) where as much as three-quarters of a stand is thinned or harvested, leading to a large range in canopy gap sizes at the forest management unit level. This is done to remove non-functional elements, and to create new opportunities in the stand in question (Van der Jagt et al., 2000).

In summary, the current focus on methods of sustainable natural forest management, the dominance and subsequent transformation of even-aged monocultural stands in the Netherlands, the financial incentive to transform monocultures into more natural forests, and the policy-supported accent on Integrated Forest Management have increased the application of gap-phase regeneration in the Netherlands. This has resulted in many mixed-species sapling communities in small and large canopy gaps, intended to provide uneven-aged mixed-species forests.

This natural regeneration will form the starting point for a new mature forest, and should in due course provide the desired forest characteristics. Regeneration in fact is the basis for the future species composition and functioning of the forest (cf. Franklin et al., 2002), which means that it ultimately must provide all of the required functions and structures. Therefore, as stated by Mosandl and Küssner (1999), the question whether natural regeneration processes lead to productive well-structured mixed-species stands is particularly important under the present-day management objectives. This question places a large emphasis on the early stages of stand development as occurrences here have a long-lasting effect on the forest. Most of the even-aged Dutch forest is coniferous (62 percent of the regular high forests), and a common forest type is the even-aged Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) forest (LNV, 2007). It makes up 11 percent of the coniferous production forests (and 6 percent of the whole Dutch forest area), which is far less than Scots pine (*Pinus sylvestris* L.) forests which occupy 59 percent of the coniferous production forests (and 33 percent of the whole Dutch forest area).

Contrary to Scots pine, the Douglas fir is an exotic tree species. It has historically been planted for wood production only (RIVM/CBS/DLO, 2003), and in even-aged monospecific stands it is associated with little biodiversity as it casts a deep shade suppressing most other vegetation. This presents an undesirable situation under current forest policy objectives, and these forests are therefore often under conversion to more natural stands. In doing so it is the intention that the application of gap-phase regeneration will ultimately lead to mixed-species stands. For this to happen the outcome of the first two to three decades of stand development is vital. Different species must establish and survive long enough to make it to the adult stages where they can gain a canopy position and reproduce. Given the competitive ability and non-indigenous origin of Douglas fir, monospecific stands of this species under transformation management would provide a good opportunity for evaluating whether the application of gap-phase regeneration will eventually lead to mixed-species stands.

Growth, competition and survival in the gap building phase as determinants of coexistence in mixed communities

The gap building phase

If the objective of close-to-nature silviculture is to establish natural mixed-species stands, then species coexistence is the relevant underlying ecological phenomenon. How multiple plant species are able to coexist at small spatial scales is one of the important questions in ecology (Wright, 2002; Silvertown, 2004). The answer to this question primarily lies in regeneration and the subsequent competitive exclusion in the gap building phase (Brokaw, 1985; Wright, 2002). The gap building phase is the period after gap formation in which natural regeneration has permanently established, up to the point that it makes the transition to young but mature forest. It includes the period in which saplings undergo self-thinning, the phase in which stem number is drastically reduced by fierce competition. As a result, the final species composition and forest structure are to a large extent determined in the gap building phase (Franklin et al., 2002), making it an important phase in stand development.

Self-thinning

Self-thinning is an important driver of stand development (Oliver and Larson, 1996). Self-thinning is the reduction in the number of individuals per surface area as the average size of these individuals gets bigger (Pretzsch, 2001), and is therefore an example of density-dependent mortality. The reduction in stem number with an increase in average diameter was already described by Reineke in his Stand Density Rule (Reineke, 1933). The relationship between average biomass and stem number was formalized by Yoda (1963) in the equation $ln(mass)=b-3/2 \cdot ln(number)$. These relationships are driven by the competition for resources and small size differences can determine the difference between survival and competitive exclusion.

However, importantly, instead of a single equation describing all species, later versions of the self-thinning equation included aspects of plant geometry and could be adapted to individual species (Lonsdale and Watkinson, 1983; Weller, 1987; Ellison, 1989). These authors found that crowding, and thus competition, is less when plants grow tall rather than wide. Whole-tree and crown architecture therefore are important determinants of self-thinning (Franco and Kelly, 1998). This points to a strong role for the competition for light in self-thinning. For example, a slender stem and narrow crown allow an efficient height growth (Poorter and Werger, 1999; Poorter et al., 2003). And expending more resources on height growth instead of horizontal expansion leads to less horizontal overlap in crowns. As a result, a given amount of biomass can be added with less attendant mortality (Ellison, 1989; Xue et al., 1999). The differences between species in plant geometry are reflected in a species-specific ontogenetic development, which should therefore play an important role in the competition for light in the self-thinning phase.

Morphology and height growth

After the establishment of multiple species, rapid height growth may allow light-demanding species to avoid being shaded by others. Slow-growing shade-tolerant species on the other hand tolerate lower light levels, so they can persist under a canopy of fast-growing species. This can give rise to vertical stratification in a developing stand (Oliver and Larson, 1996). This

describes a classical pioneer-climax dichotomy in which slow growing shade tolerants are overgrown by fast growing light demanders, allowing them to coexist (Swaine and Whitmore, 1988). Important factors in a vertical stratification between species are slenderness and height growth rate.
Also crown properties can influence growth and survival (Sterck and Bongers, 2001; Sterck et al., 2003). For example, crown architecture can yield a very open crown structure (e.g. *Betula* spp) which, together with leaf characteristics, determines light capture and attenuation. As a result, crown properties play an important role in the competition for light, and, by reducing light levels below the crown, influence succession (Horn, 1971). The underlying mechanism is that competition for light is asymmetric (see next section) and is mediated by carbon allocation to different structures, e.g. a wide crown or a tall stem (Schwinning and Weiner, 1998). Small differences in height result in large changes in the intensity, direction and quality of irradiance, and may exercise a critical effect on growth and survival (Grime, 2001). Crown characteristics and height growth are therefore important factors in the competition for light.

Competition for light

In self-thinning, the correlation between mortality and crown geometry (Lonsdale and Watkinson, 1983; Weller, 1987; Franco and Kelly, 1998) suggests that the reduction in individuals is mainly driven by the competition for light. That is to say, species with narrow crowns show less density-dependent mortality than species with wide crowns. The strong role for the competition for light is supported by the vertical stratification in developing stands through differences in height growth rate and shade tolerance. This similarly suggests that the competition for light, leading to a partitioning of the light gradient, is an important factor in species' coexistence (Poorter and Arets, 2003). The competition for light in the gap building phase will therefore be the main focus in this thesis, even though the competition for water and nutrients also will play a role.

Competition is defined as an interaction between individuals brought about by a shared requirement for a resource, leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned (Begon et al., 1996). This definition is based in resource limitation and does not focus on particular mechanisms of competition (e.g. low-resource tolerance), but broadly incorporates all resource-mediated processes that lead to negative effects on other individuals.
Competition can be either symmetric or asymmetric. Competitive symmetry means that resource capture between two competitors is proportional to their body size, and asymmetry means that one individual captures disproportionally more. The competition for light is therefore inherently asymmetric (Schwinning and Weiner, 1998) because a plant that is only slightly taller can pre-empt the resource and shade a marginally smaller

neighbor, thereby exerting a competitive influence (Goldberg and Barton, 1992).

In the gap building phase, in theory, if all saplings would have the exact same size, they would intercept the same amount of radiation as no tree overtops another (not accounting for species' differences in morphology). This situation would lead to stagnation, i.e. trees slow down in diameter and height growth (Oliver and Larson, 1996). This is however rarely the case as many factors can lead to initial size differences. Such factors are early arrival, differences in neighborhood density, microsite variation and genetic differences (Huston, 1994; Oliver and Larson, 1996). Genetic differences entail differences in morphology (e.g. the allometric relationship between trunk diameter and tree height, or differences in the allocation to support mass versus leaf mass), as well as growth rate (King, 1994, 2005).
The resulting differences in height are important given the asymmetric competition for light. Slender trunks for example facilitate rapid height growth by lowering the biomass needed to achieve a given height (King, 1981). The resulting differences in height can have a critical effect on light capture, and therefore ultimately growth and survival (Kohyama, 1993; Grime, 2001; Sterck et al., 2003). For a tree it is beneficial to either grow faster in height than its neighbors, or on the other hand to be sufficiently shade tolerant. This is based in two alternative mechanisms of plant competition: resource depletion and resource pre-emption (Tilman, 1990; Grime, 2001; Weigelt and Jolliffe, 2003). Such mechanisms of competition themselves are not researched in this thesis however.

Once a canopy is present above or next to a tree's own canopy, the characteristics of the surrounding tree crowns (for example the number of leaf layers) will determine the amount of light that is transmitted and available for photosynthesis. If light levels are sufficiently reduced by the surrounding foliage, the lower branches in a canopy will have a negative carbon balance and die (Oliver and Larson, 1996). In the end, if a tree cannot grow tall enough to stay in the main canopy, and unless it is sufficiently shade-tolerant, it cannot capture enough light and the whole tree will die (Givnish, 1988). The effect of crown characteristics on light transmission is often found to have a strong effect on growth and survival (Küppers, 1989; Canham et al., 1994; Yokozawa et al., 1996).

Growth, survival and coexistence

The forest architecture hypothesis states that the coexistence of species is promoted by a vertical stratification that is based in species' differences in growth rate and shade tolerance (Kohyama, 1993). This means that two (groups of) species can coexist because fast-growing light demanders overtop slow-growing shade tolerants. Growth in full light is higher in light-demanding species due to a higher net assimilation rate and leaf area ratio (Poorter, 1999; Portsmuth and Niinemets, 2007). Survival in the shade is higher for shade-tolerants due to a lower whole-plant light compensation point and a higher carbohydrate storage (Walters and Reich, 1999; Poorter and Kitajima, 2007). In explaining coexistence the forest architecture hypothesis thus incorporates the competition for light, leading up to a partitioning of the light gradient (Poorter et al., 2003) that in turn is based in physiological and morphological characteristics.

In the Douglas fir forests that will serve as a case-study in this thesis, natural regeneration in gaps mainly consists of Silver birch (*Betula pendula* Roth.), Douglas fir, Scots pine, and Japanese larch (*Larix kaempferi* Carr.). These four species differ in physiology and morphology, notably their height growth, slenderness, crown size and shade tolerance. Such differences potentially allow species coexistence (Yokozawa et al., 1996). Also Pronk (2004) theoretically demonstrated that differences in height growth contribute to niche differentiation, and in the end allow for the coexistence of multiple species. As Silvertown (2004) states: niche differentiation, and specifically the partitioning of the vertical light gradient through a trade-off between growth rate in high light and survival in low light, is not the only mechanism of coexistence, but it is important in understanding which species can be expected to segregate into stable plant communities. In investigating coexistence in the gap building phase, I will therefore focus on vertical stratification according to height growth and shade tolerance, and investigate whether this promotes a situation of niche differentiation that enables coexistence.

Objective

There is much scientific, societal and political attention for the transformation of even-aged single-species forests under a clearcut system, to uneven-aged mixed-species forests under a group-selection system. Natural regeneration in canopy gaps often forms the starting point for such transformation. After group harvesting, seedlings will establish, grow and compete, and in the end will develop into the new mature cohort. During this development towards mature forest, the stem exclusion phase is the developmental phase where competitive exclusion occurs and future forest composition is determined.

> *It is the overall objective of this thesis to investigate species coexistence in gap-phase regeneration as an important objective in close-to-nature silviculture. More specifically, I will test whether, after the application of gap-phase regeneration and in the stem exclusion phase, species stratify in height according to their height growth and shade tolerance, and in doing so reach a situation of niche differentiation that promotes their coexistence.*

This research only looks at species performance under natural conditions, i.e. where growth and competition are not directly interfered with through management, and focuses on the natural processes that underlie all particular approaches to close-to-nature silviculture (growth, competition and mortality in dense, naturally established communities). Given the importance of the sapling stage, I will concentrate all research efforts on patches of natural regeneration undergoing self-thinning. Specifically, I will limit field research to even-aged Douglas fir stands under transformation management, and occurring on the dry sandy soils in the Netherlands. Natural regeneration in these forests mainly consists of Silver birch, Douglas fir, Scots pine and Japanese larch, which are therefore the focal species for this research.

On a slightly wider scope the aims of this study are:

1. To investigate the international socio-political framework for close-to-nature silviculture.
2. To evaluate species performance in mixed-species sapling communities. With species performance is meant the ability to maintain oneself, i.e. to grow, to compete, and to persist in mixture with other species.
3. To explore the implications of this performance for the long-term coexistence of species.

Definitions

Close-to-nature silviculture

Close-to-nature silviculture is loosely defined as any approach to forest management that aims to increase the naturalness of the forest (e.g. by creating a mixed-species composition and a mosaic of stand developmental phases) by initiating and making use of natural processes in forest management (e.g. natural regeneration after group harvesting, self-thinning rather than non-commercial first thinnings), while allowing natural dynamics (e.g. natural senescence, gap creation by wind-throw) to take place, in order to provide multiple forest functions (mainly wood production, biodiversity conservation and recreational values). This does not exclude area-based management interventions like small-scale clearcutting of non-indigenous species, or the planting of desired indigenous species. Transformation management aimed at transforming even-aged monocultures into mixed uneven-aged forests by group harvesting is taken as a preliminary phase in close-to-nature silviculture.

Gap-phase regeneration

This is the natural establishment of trees after the main canopy has locally been removed, leaving a gap in an otherwise continuous canopy, and also includes the release of advance regeneration that was already present before gap formation (Brokaw, 1985). Canopy removal can stem from natural causes or from harvesting, and gap size can range from a patch created by the removal of a single tree, to large patches created by the removal of many trees (equivalent to a small-scale clearcut).

Gap building phase
After gap formation a number of subsequent developmental phases can be recognized leading up to new mature forest. These phases are 1) the gap phase, 2) the building phase, and 3) the mature phase (Clark and Clark, 1992). In this thesis I will use the term gap building phase for the period of time in which natural regeneration has permanently established, up to the point that it makes the transition to mature forest. Using the terminology from Oliver and Larson (1996), the gap building phase includes the stand initiation phase and the stem exclusion phase.

Stem exclusion phase
This stand developmental phase starts when a patch of newly established trees makes the transition from open growth conditions to a situation characterized by canopy closure and a subsequent strong competition for light. New individuals no longer can establish successfully, existing individuals expand their biomass at the expense of the growth of other individuals, and species manifest their species-specific growth characteristics (Oliver and Larson, 1996). The initial high stem density leads to high mortality and a strong reduction in stem number. The stem exclusion phase includes the sapling stage (*in Dutch:* 'dichte fase') and pole stage (*in Dutch:* 'stakenfase'), and ends when mortality levels off, new individuals establish in the understory (trees, shrubs and herbs), and the remaining trees markedly increase in diameter leading to a lower height-diameter ratio.

Competition
Competition is an interaction between individuals, brought about by a shared requirement for a resource, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned (Begon et al., 1996).

Sapling
For the purposes of this thesis a sapling is defined as an individual growing in the sapling or pole stage, having a height of approximately 2 to 10 m, and an age of approximately 5 to 20 years.

Thesis outline

Chapter 2 describes the international socio-political framework for Ecosystem Management (EM), which can be seen as an overall management approach in which close-to-nature silviculture takes place. The picture of EM that emerges from this review at the international level is then compared with the national policies from three case study countries: Germany, Finland and Spain. This comparison aims to investigate whether there is a consistent reference image for EM which is translated from international agreements to national policies, and that is ultimately used for goal-setting in forest management.

With the socio-political framework for close-to-nature silviculture outlined, the thesis then makes the transition to biophysical field research by investigating species performance after establishment in mixed-species sapling communities in canopy gaps.

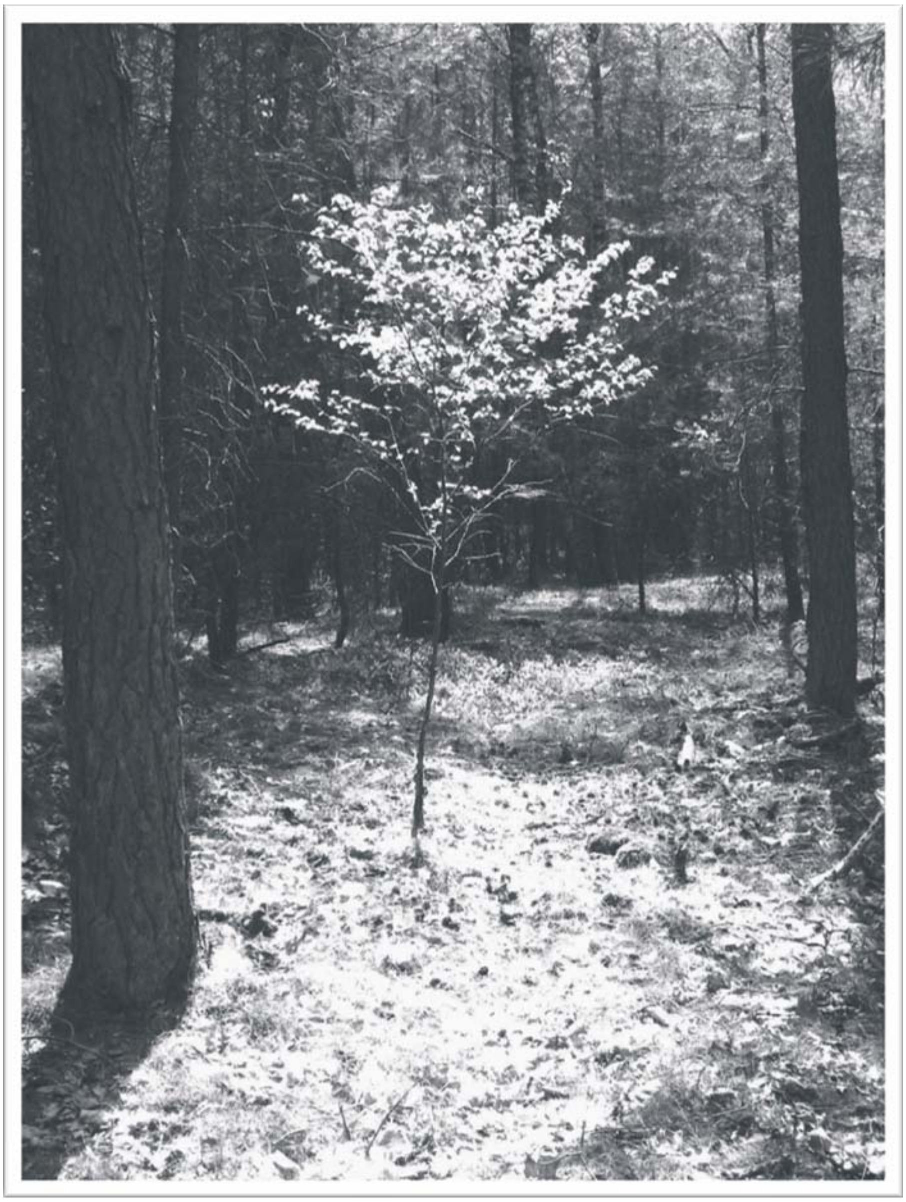
Chapter 3 develops allometric biomass equations that estimate aboveground biomass as a function of DBH. This is done for the four species that are central to the remainder of this thesis: Silver birch, Douglas fir, Scots pine, and Japanese larch.

Chapter 4 analyses the architectural contribution to a sapling's height. The following questions are addressed: 1) do saplings differ in height for equal DBH or aboveground biomass, and 2) what is the role of slenderness and biomass partitioning in height differentiation. In this chapter static sampling data are compared with data on annual diameter and height growth. Based on the inferred stratification in heights, next to reported species' light requirements, a hypothesis is developed on the interspecific competition for light.

Chapter 5 quantifies vertical stratification between saplings, and analyses the competitive effect of neighbour species on target species in two sapling communities of ~5 and ~15 years old. The total foliage mass as well as the foliage mass density of neighbor trees are taken as factors exerting a competitive pressure. The relative crown depth of target trees is taken as the response variable. We subsequently test whether species vertically stratify according to their light demand, and whether a higher foliage mass (or density) results in a stronger competitive pressure.

Chapter 6 investigates the effect of light availability on the growth and survival in saplings of the studied species. Long-term and short-term radial growth responses in relation to crown positions are addressed, as well as the probability of mortality as a function of radial growth. Results are used to infer consequences for the competitive exclusion or coexistence of species.

Chapter 7 summarises the key findings, connects the different chapters, and places the results in the bigger picture of the application of close-to-nature silviculture in the Netherlands.



CHAPTER 2

Interpretation and implementation of Ecosystem Management in international and national forest policy

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Ecosystem management, policy buzzword or scientific approach to natural resource management?

Ecosystem Management (EM) is a concept frequently encountered within the scientific literature and within policy documents. Many different attitudes towards and meanings of EM can be discerned. In political documents, EM is used as a political concept referring to certain desired attitudes towards ecosystems. On the other hand, examples in the scientific literature (e.g. Christensen et al., 1996; Kohm & Franklin, 1997) refer to EM as a scientific approach to natural resource management. For some, this diversity in attitudes towards and meanings of EM is problematic. For example, Goldstein (1998) refers to EM as a buzzword without true meaning. Furthermore, several authors (e.g. Wilcove & Blair, 1995; Goldstein, 1998; Yaffee, 1999; Newton & Freyfogle, 2005) have argued that the different meanings and values assigned to EM lead to its subjective and problematic application or evaluation, and that without agreement on the concept and its application there is the risk that every type of management can be called Ecosystem Management. It then merely provides nominal justification for practices that have little to do with Ecosystem Management, and therefore does not lead to the improvements in management that the concept aims for. The vagueness of the term allows people to make of it what they want when there are no clear procedures for assessing whether or not management goals have been met. This ensures that anyone can implement it according to their own views (Wilcove & Blair, 1995; Goldstein, 1998).

Despite unclear definitions and vague meanings, EM appears to be one of the current leading approaches in forest policy (e.g. UNEP, 2000) and management (e.g. Sayer et al., 2004). Therefore, in order to gain a deeper understanding of current forest policies and management approaches, it is crucial to look at how the concept of EM is used and in what ways and to what extent interpretations and meanings actually differ or converge.

In the next section we will present a qualitative review of the literature about EM and about concepts related to EM. We will identify some common characteristics of EM, leading to a general description, not to a precise definition. This general description will then be used to analyse the uses and interpretations of EM in several international forest policy documents and in national forest policy documents of Finland, Germany and Spain.

Ecosystem Management and related concepts

The term Ecosystem Management originated in North-America (Grumbine, 1994). Haeuber (1998) has linked the emergence of EM to initiatives based on a systemic approach to managing natural resources at a landscape scale such as the biosphere reserves in the 1970s, the Great Lakes water quality agreement signed in 1972 and the management of the Greater Yellowstone Ecosystem in the 1960s. Since its emergence, EM has found its way into international policies (e.g. UNFCBD, 2003b). Through the Biodiversity Convention, it has also entered forest policies in Europe (e.g. MCPFE, 2000). EM is however more than a technical management approach. It deals with the role of man in nature and the place and functioning of natural resources within society (cf. Christensen et al., 1996). It contrasts with traditional forest management which mainly focuses on optimizing the provision of goods and services (Grumbine, 1994). In EM it is important to find a new relationship between man and nature, to maintain ecosystem integrity while specifically considering the human factor, i.e. to go beyond a focus on the provision of goods and services (Yaffee, 1999). This is termed “reframing environmental values”, and regards nature as more than a life-support system for humans, assigning intrinsic value to it. Ecosystem Management is therefore, most importantly, more than an extension of traditional resource management with new environmental objectives (Grumbine, 1994).

Several arguments have been used to advocate Ecosystem Management. Bengtsson et al. (2000) have argued that in order to achieve sustainability it is necessary to incorporate ecosystem dynamics into forest management, e.g. small and large disturbances, presence of dying and dead trees, shifting mosaics of species and ages. In order to maintain the assigned forest functions in light of these dynamics, management strategies must focus on persistence and stability of the ecosystem (Führer, 2000). Holling and Meffe (1996) have stated that it is therefore important not to counteract natural developments. This is supported by Knapp (2003), who states that conservation should not be aimed at compositional stasis in an environmentally dynamic world. These overall objectives can be reached through small-scale management aimed at heterogeneity, preserving the environment and biodiversity (Bengtsson et al., 2000).

What is important therefore is the objective to follow natural variability and dynamics, as well as to incorporate the full socio-economic context into management (Grumbine, 1994; Christensen et al., 1996). These are essential characteristics of Ecosystem Management.

It was argued earlier that EM is a vague concept lacking a clear definition, but according to Haeuber (1998) there is also common ground: "despite a confusing proliferation of definitions, a generally accepted set of Ecosystem Management principles, or components has emerged". This set includes social and economic elements such as the principle of sustainability (ecological, socio-economic and cultural), the recognition that people cannot be separated from nature, that EM is a social process in which human values are important and that EM requires participatory decision making processes that include different stakeholders (Haeuber, 1998). A similar definition is given by Grumbine (1994): ”Ecosystem Management integrates scientific knowledge of ecological relationships within a complex socio-political and values framework toward the general goal of protecting native ecosystem integrity over the long term”. And also by Christensen at al. (1996): ”Ecosystem Management must include the following: […] sound ecological models […], understanding complexity and interconnectedness,

[…], acknowledgement of humans as ecosystem components, […]”. These examples show that it is the combination of technical-scientific and social elements that is at the heart of EM. For the remainder of this paper this will serve as a descriptive 'definition' of EM.

This paper will also include references to concepts related to EM. The first one is the term Ecosystem Approach (EA). This concept is often used in a more general way than EM (Maser, 1994), but for our purpose this is not a relevant distinction. The second related concept is Ecosystem Stewardship (ES). When considering the way that Kennedy et al. (2001) describe this concept, i.e. management aimed at sustainable, healthy, diverse and interrelated socio-economic, cultural, and environmental systems, it becomes clear that this is a similar concept as EM. A third related concept is Sustainable Forest Management (SFM). As for EM, no shared definition exists for SFM. Schanz (2004) has identified as much as fourteen different categories of definitions of the concept of sustainable forest management. It is a dynamic concept and the meaning of SFM differs in different political contexts with different values and interests at stake (Schanz, 2004). SFM has evolved from a concept referring to a management regime aimed at achieving a sustained timber yield to a concept that has been broadened to incorporate ecological and socio-cultural aspects (Maser, 1994; Schanz, 1996; Rametsteiner, 2000). Finally, this paper will also consider the concept of Adaptive Management. AM is often seen as a component of EM (Grumbine, 1994; Christensen at al., 1996; UNEP, 2000). It is based on two notions: first, management of the resource must continue even when little is known about the consequences. Second, natural systems and social systems are interdependent, i.e. as the resource changes so does its exploitation (De Boo & Wiersum, 2002). It thus forms a continuous cycle of management based on studying, planning, executing, monitoring, evaluating and adjusting, and in itself it is not limited to specific aspects of management. In that way natural, human or human-natural systems are interconnected in continual adaptive cycles of growth, accumulation, restructuring, and renewal (Holling & Meffe, 1996; Holling, 2000). AM is not a fixed solution but a flexible approach to deal with change.

As these four concepts all include technical-scientific as well as social elements, we consider them related to EM. Although we acknowledge nuances and differences between the concepts, it is the combination of these two elements, and the extent to which we can recognize this combination in policy documents, that we are interested in. Therefore, we will include in our analysis references made to EM as well as to the Ecosystem Approach, Ecosystem Stewardship, Sustainable Forest Management and Adaptive Management.

Analyzing the implementation of Ecosystem Management in forest policies

An important rationale for studying the implementation of EM, given its observed vagueness, lies in the fact that by doing so we gain more insight in its different meanings, interpretations and uses.

In traditional policy-science literature that conceptualises policy processes as linear and consisting of separate phases (e.g. Winsemius, 1986; Hoogerwerf, 1989), implementation is regarded as the phase after policy development and setting. In many implementation studies (e.g. Bressers & Hoogerwerf, 1991) differences between goals and effects of policies and differences in implementation practices have been observed. Importantly, the labelling of these differences as implementation gaps and failures makes clear that these studies consider the differences to be problematic. Furthermore, the way in which these studies explain the observed gaps and failures by referring to unclear policy goals seems to imply that implementation problems could be avoided if only policy goals were clear and unambiguous. We take issue with such a conceptualization of policy processes as it fails to acknowledge and recognize the interpretative space that policy goals necessarily afford and the context specificity of implementation practices. Context is very relevant here as many authors have described how transportation processes (of things like knowledge, concepts, approaches or policy goals) from one context into another, as is the case with implementation, necessarily involve reinterpretations (Boogerd, 1997; Turnhout, 2003; Turnhout & Leroy, 2004) resulting in a diversity of implementation practices.

Considering implementation as reinterpretation makes clear that when analyzing the implementation of EM in policy documents, differences in interpretations of EM are not surprising. However, in order to gain a deeper understanding of the interpretations and uses of EM it is important to analyse how and to what extent implementation differs. We will use the general description of EM (including EA, ES, SFM and AM) that we have developed in the previous section as a basis for our analysis. We wish to emphasize here that we do not consider this general definition of EM to be the only correct interpretation of EM. It serves only to characterize the implementation of EM and to characterize differences in implementation. This means that we will specifically focus on to what extent technical-scientific and social elements can be recognized.

We will study the implementation of EM on two levels, the international level and the national level. On the international level, strategic international and European policy documents were selected that contained guiding principles or descriptions of desired futures. The selected documents include Strategies as well as Principles and Indicator Schemes. For our analyses on the national level, key policy or legislative documents such as Forest Acts and National Forest Programmes (NFPs) of three European countries (Germany, Finland and Spain) were selected. These countries were selected because they represent three very different regions in Europe in terms of forest cover, forest characteristics, and the (historical) importance of forestry to society (Stanners & Bourdeau, 1995; MCPFE, 2003). We have analysed the selected documents paying attention to those statements that refer to general aspirations regarding the management of natural resources or desired futures. Furthermore we have looked for statements that refer to EM or its related concepts, and that contain the interpretations and meanings of EM (or its related concepts).

In total, we feel that our selection of international and national documents and our selection of countries provides a good, although necessarily incomplete, overview of the diversity in meanings and interpretations of EM. In addition, analysing the implementation of EM on two levels provides interesting possibilities for comparison. As the international policy documents are assumed to give direction to national policy documents we can consider the national policy documents as implementations of international policy documents. It will be interesting to see if we can identify differences in interpretations and meanings of EM between the two levels.

Ecosystem Management in international forest policies

The results of our review of international policy documents are listed in Table 2-1. The second column presents the interpretations and meanings of EM that we identified in the selected documents. Table 2-1 shows that both social as well as technical-scientific elements can be recognized. In the strategic documents, for example, references are made to complexity, broad ecosystem functions, socio-economic aspects and intrinsic non-use values. The Principles and Indicator Schemes present a comparable picture and include references to biodiversity conservation and ecosystem functioning, as well as socio-cultural aspects.

Such similarity has also been observed by Mc Donald and Lane (2004) in their comparison of the Montreal Process-, the Ministerial Conference on the Protection of Forests in Europe- (MCPFE), and the International Timber Trade Organisation- (ITTO) Criteria & Indicators. Criteria for SFM appear quite similar and generally incorporate the conservation of biological diversity, the maintenance of productive capacity, the maintenance of ecosystem health, the conservation and maintenance of soil and economic benefits, and the presence of a legal, institutional and economic framework for management (McDonald and Lane, 2004).

We conclude that the selected international policy documents together seem to present a relatively homogeneous picture of the implementation of EM as a concept that includes social as well as technical-scientific elements. It should be noted here that, given our focus on interpretation and context specificity, these results are somewhat surprising. We will further go into this issue in our comparative section, after presenting the results of our review of national policy documents.

Table 2-1. Key words and phrases from the selected international forest policy documents

Source	Key words and phrases
UNCED Forest Principles[a]	Forests' multiple values and multi-functionality must be maintained in a holistic and balanced manner. Forests are unique and complex ecosystems of value to local communities and the environment as a whole. Social, economic, ecological, cultural and spiritual needs must be met, now and in the future. All aspects of environmental protection and social and economic development should be integrated. Education, training, science, technology, economics, anthropology and social aspects are essential to sustainable forest management. Needs comprise wood and wood products, water, food, fodder, medicine, fuel, shelter, employment, recreation, habitats for wildlife, landscape diversity, carbon sinks and reservoirs, and other forest products.
Follow-up to the UNFCBD (CoP 1 to 6)[b]	Biodiversity conservation and Sustainable Forest Management must be addressed with a holistic ecosystem approach. The CoP emphasizes the importance of combining conservation, management and sustainable use of forests. Forests and forest biological diversity play important economic, social and cultural roles in the lives of many indigenous and local communities. The Conference of the Parties recognizes the need to develop and implement methods for sustainable forest management which combine production goals, socio-economic goals, and environmental goals. Consider the economic (monetized and non-monetized) benefits, the environmental services and non-consumptive values, including the important cultural, religious and recreational values of forests.
Pan-European Biological and Landscape Diversity Strategy[c]	Sustainable use and conservation must be incorporated into management. Sustainable management makes optimum use of social and economic opportunities. Ecological integrity must be maintained in order to protect habitats and ensure species survival. Enhancement of an indigenous tree species composition Intensive silviculture and monocultures are challenges to be addressed. Integrated approach and a Best Environmental Practice incorporating the forests' multiple functions.

(Table 2-1 continued)

Community Forestry Strategy[d]	Key issues in forestry are *inter alia* the protection of the natural environment; contributing to rural development; maintenance of social and recreational functions; improvement of ecological, economic and social sustainable forest management. Maintain dead wood and key micro-habitats. Focus on natural regeneration and a native species composition. Conservation takes place in sustainable management systems. Maintain forest health and vitality, regenerative capacity, resistance and adaptive capacity.
MCPFE Criteria, Indicators and Operational Level Guidelines for SFM[e]	Multiple-use forestry aiming at multiple forest functions. Maintain health, vitality, stability, resistance and adaptive capacity. Promote silvicultural practices emulating nature. Use preferably native species suited to local conditions. Maintain natural structures and processes as well as genetic, species and structural diversity. Apply natural regeneration in uneven-aged mixed stands. Maintain dead or hollow trees, old groves and rare species. Take into account all socio-economic functions of the forest like rural development, the recreational function and aesthetic values.
FSC Principles and Criteria[f]	Acknowledge all social, economic, ecological, cultural and spiritual functions of the forest, now and in the future. Enhance long-term well-being of local communities. Forest management that is economically viable, while taking into account the full environmental, social, and operational costs. Maintain ecological functions, ecosystem diversity and integrity, forest succession, natural cycles.
CIFOR's Criteria and Indicators[g]	Maintain biodiversity, ecosystem function and integrity. Incorporate social and cultural aspects in the sustainable yield of goods and services. There is a recognizable balance between human activities and environmental conditions. Forests have a multifunctional role. Management incorporates all stakeholders and all forest functions such as timber, non-timber forest products, ecology and well-being of local populations.

a: UN-GA, 1992
b: UNFCBD, 2003a, b
c: CoE, 1995
d: EC, 1998
e: MCPFE, 2000
f: FSC, 2004
g: Prabhu et al., 1998

We have additionally observed strong similarities between the interpretations of EM on the international policy level and the deliberations on EM (specifically SFM) in the scientific literature (see Maser, 1994; Holling & Meffe, 1996; Toman & Ashton, 1996; Bengtsson et al., 2000; Farrell et al., 2000; Führer, 2000; Holling, 2000; Gamborg & Larsen, 2003; Schanz, 2004). Overall, on the international level there is an apparent homogeneity in the approach to EM and SFM stipulating that forests no longer have a commodity function only, but also incorporate intrinsic non-use values, e.g. preservation of autogenic evolutionary processes. Emphasis is placed on the fact that management will always have to incorporate the multiple functions of the forests, e.g. biodiversity, carbon sequestration and recreational values, and when this is financially unrewarding it should be stimulated by incentives from national level policies.

Ecosystem Management in national forest policies

The results of our review of national policy documents are listed in Table 2-2. The second column presents the different interpretations and meanings of EM that we identified in the selected documents. To add structure, we have grouped our results around the three central components of forest management (cf. IUFRO, 2004), i.e. regeneration, utilization and conservation. This provides the ability to compare and differentiate between countries.

There are large differences between countries in their forest policy objectives. Documents differ in the level of detail that they provide, e.g. from very general to very specific stand characteristics, and in the way that the international policy objectives are filled in, e.g. the chosen approach to EM.

Table 2-2. Key words and phrases from national forest policies and legislation

	Germany[a]	**Finland**[b]	**Spain**[c]
Regeneration (*inter alia* tree species composition, genetic variability)	Tree species suited to site conditions. Favour natural regeneration and indigenous planting material. Preservation of genetic diversity. Use non-indigenous species only if this does not lead to site degradation, and mixed with indigenous species. Maintain tree species diversity, also non-commercial species.	Natural regeneration to be kept at a share of about 32% because of cost reduction, but only if conditions are suitable (avoiding risk of failure and longer rotation lengths).	Facilitate genetic exchange through corridors that increase connectivity between forest areas.
Utilisation (*inter alia* the use of natural processes, considering climate change impacts, harvesting and tending)	Increase the amount of forests under close-to-nature forestry. Increase mixture, vertical structure, share of broadleaves.' No clearcutting but selection cutting. Low impact harvesting and tending. Tending forest edges for landscape amenity. Hunting appropriate to forest and game. Conversion of large-scale conifer monocultures in mixed forests.	Ecosystem management of commercial forests. Felling to be performed so that it promotes either growth (potential), or the formation of a new stand. Increase the amount of forests that receives first thinnings in order to augment the harvest of commercial timber. Fertilisation to accelerate growth.	Increase structural diversity. Cleaning of forests with high density and lack of growth. Increase the percentage of mixed forests. Multiple use aimed at social, economic and ecological functions.

(**Table 2-2 continued)**

Conservation (*inter alia* dealing with invasive species, insects and disturbances, risk management, climate change adaptation)	Increase forest resistance by avoiding the use of chemicals. Soil protection by refraining from fertilisation and lowering the ground water table. Protection and maintenance of rare or endangered species and habitats. Retain old trees and dead wood. Increase standing stock and apply close-to-nature forestry for increasing carbon storage.	Key habitats are identified and forest management will ensure preservation of the prerequisites for maintaining these sites. Felling in forests of special importance will be carried out in accordance with the nature of the site. Felling in a protection forest area only with approval of a Forestry Centre. Groups of trees and decayed trees to be left in regeneration areas.	Increase the forests' capacity for carbon sequestration through silviculture. Forest conservation through hydrological restoration and protection against fire, pests and diseases. Avoid fragmentation.

a: Bundesministerium für Ernährung, Landwirtschaft und Forsten 2000, 2001
b: Ministry of Agriculture and Forestry 1996, 1999
c: Ministerio del Medio Ambiente 1998, 1999, 2002

In its policy documents Finland specifically mentions EM, as well as the terms sustainable forestry and sustainable management. This however is filled in with strongly production-oriented management objectives. The reviewed Finnish policy documents refer to, and therefore implement, the United Nations Conference on the Environment and Development (UNCED), the MCPFE process, and European Union (EU) policy (Ministry of Agriculture and Forestry 1996, 1999).

The policy documents from Germany refer to the concept of SFM, but mainly focus on close-to-nature silviculture. The reviewed German policy documents however implement the same policy framework, i.e. the UNCED and its follow-up, the MCPFE process and, specifically, the EU Forestry Strategy (Bundesministerium für Ernährung, Landwirtschaft und Forsten 2000, 2001).

The reviewed policy documents from Spain use the terms SFM and forest multifunctionality, but do not elaborate on specific stand level details. The documents refer to the UNCED and its follow-up, the MCPFE process and the EU Forestry Strategy and related EU policy (Ministerio del Medio Ambiente 1998, 1999, 2002).

The large differences in implementation exist even though all three countries are party to the UNCED conventions, member states of the EU as well as member of the MCPFE process. This also becomes clear from the references that are made to international policy. Therefore, the overall international policy framework that they have to implement (e.g. see Table 2-1) is the same, and has been for years.

Implementation differences between countries may be further understood by taking into account the history, physical condition of the forests, and the status of forestry in these countries. The exact relationship between the state of forests (and forestry) in a country and a country's forest policy is complex. It is not linear and causal and cannot be used to directly explain differences in policy. It does however offer background information for the interpretation of policies. Table 2-3 therefore describes some characteristics of the national forest estates of the case-study countries.

From Table 2-3 it can be seen that Germany has a high share of coniferous forests (for a Central-European country), indicating the widespread creation of plantations in the eighteenth and mainly nineteenth century (Huss, 1990; Stanners & Bourdeau, 1995; Farrell et al., 2000). That forest management is an important economic activity is clear from the fact that all forests are under management, that Germany has the highest standing volume per hectare, and the highest volume increment (Table 2-3). Also carbon sequestration is an important aspect of forest management as Germany has the largest carbon stock. Central-Europe has a very long forestry tradition and is the place where as a result of the high share of coniferous forests, historically close-to-nature forestry developed (Otto, 1993b; Farrell et al., 2000; Gamborg & Larsen, 2003). Given this setting, close-to-nature forestry is now elaborately incorporated in German policy documents.

In Finland, where the development of forestry has already shown a focus on intensification of forest management (Stanners & Bourdeau, 1995), wood production still is the dominant rationale in policy documents. As can be seen in Table 2-3 forests are an important part of the land area of Finland. These boreal forests additionally have a naturally high share of coniferous timber species. Most forests are under management, making forest management an important activity. The reported intensification of forest management is reflected in the fact that annual volume increment is largely harvested. Finland, like Germany, also has a large carbon stock. Production-oriented management objectives are now specifically incorporated into policy, but regarding other forest functions, e.g. carbon sequestration, no great level of detail in management activities or forest characteristics is given.

Table 2-3. National forest characteristics per country, adapted from MCPFE (2003)

Characteristic [related characteristic] (unit)	**Germany**	**Finland**	**Spain**
F [OWL] (1000 ha)	10740 [0]	22032 [850]	13656 [12611]
F [OWL] (% total)	30 [0]	65 [3]	27 [25]
CON - BL – MIX (% Forest)[a]	56 - 25 - 18	80 - 8 - 12	43 - 38 - 18
FOWL managed (%)	100	85.6	68
stem volume (m3 ha-1 Forest)	268	100	44
gross annual increment Forest [annual felling] (Mln. m3 o.b.)[b]	101 [48.6]	79 [67.5]	30 [12.6]
Felling as percentage of increment	48.2	85.3	42
carbon stock woody biomass (Tg C)	920	662.59	186.69
area forest fires (% FOWL)	0.005	0.002	0.5

In Spain, where forestry and wood production are not as important as in more temperate and boreal regions of Europe (Stanners & Bourdeau, 1995), the reviewed policy documents are not as specific as those of Germany and Finland, and a more general objective of multifunctional forest management is adhered to. Forests in Spain occur often as open woodland rather than closed forest, and relatively few of the forests are managed (Table 2-3). Comparatively, they have a low volume and low volume increment and yield little timber harvest. These forests contribute little to carbon sequestration, their fire risk however is relatively high. Forestry therefore is not such an important activity as compared to Germany and Finland which is reflected in the lack of elaboration on specific stand level management in policy documents.

Despite these differences the three countries have in common that socio-cultural elements are lacking. The central concept in all policy documents is multifunctional forest management including references to socio-economic aspects such as recreational values, landscape amenity, protective functions and the economic function. The core statements however (Table 2-2) do not appear to go beyond the provision of goods and services and do not deal with reframing environmental values. There is little specific mention of incorporation of the economic and societal context (e.g. market distortions, incentives, internalization of costs and benefits, incorporating stakeholders, planning and decision making), nor of the incorporation of the environmental effects of management (e.g. monitoring, adaptive management, autogenic processes, conservation of ecosystem structure and functioning). The implementation is restricted to technical-scientific elements only. The fact that the studied national documents, especially the Finnish ones, do refer to the concepts of EM and SFM makes clear that indeed the unclear meaning of EM allows everyone to be inspired by the concept.

Comparative analysis on the implementation of the Ecosystem Management concept in international and national policy documents

We have seen that on an international level there are many similarities in the interpretations and meanings of EM. Furthermore, all selected documents include technical-scientific as well as social elements. The focus is on a natural forest management which is more than a simple multiple-use forestry that focuses on the use by society, i.e. maximising production of goods and services. The selected policy documents deal with intrinsic non-use values, and ecosystem properties not exploitable by man.

The review shows however that this relatively coherent international policy is not uniformly translated to forest management objectives in national level policies. The three countries do mention EM and related concepts but the way they deal with the concepts differs. Finland fills in the concept of EM with production-oriented objectives. Germany has a strong orientation on close-to-nature silviculture and therefore has the highest apparent agreement with ecosystem management but that does not go beyond the stand level and no reference to Ecosystem Management is actually made. Spain presents very general objectives only. National forest policies appear to adhere to traditional management regimes, i.e. a nationally institutionalised management aimed at an optimal provision of goods and services (cf. Grumbine, 1994).

Despite these differences, there is one important similarity. In the studied documents of the three countries no specific references could be found to the social elements involved in forest policy and management. Even though the countries have agreed internationally to EM, their national level policy objectives do not appear to have changed dramatically. Especially the Finnish documents, which refer explicitly to EM, might indicate an example of relabelling business-as-usual practices with the concept of EM (cf. Yaffee, 1999).

When we compare the international and the national level we see first of all a homogeneous picture on the international level versus diversity in interpretations and meanings of EM on the national level. Given our focus on interpretation and context, especially the international homogeneity is surprising. Based on our starting points we can speculate that perhaps the contexts in which these different documents were developed en negotiated were relatively similar. Although this definitely requires further research, we might consider the possibility that it is a relatively small group of people that are involved in developing these documents. This group may even constitute an epistemic community, whose members share scientific ideas as well as political beliefs. This might help understand the similarities we have observed between the interpretations of EM in the selected international policy documents and those in the scientific literature. An example of the dominance of such epistemic communities in international (environmental) policy has been observed by Haas (1989).

A second difference between the international and the national level concerns the inclusion of both social and technical-scientific elements on the international level versus a dominance of only technical-scientific elements on the national level. This difference is less surprising in our view. Integrating different (technical and social) functions of natural resources is a challenge on every policy level. However, it has been documented (e.g. Turnhout, 2003) that on higher policy levels compromises can be made using pacifying strategies such as the involvement of experts or the adoption of shared concepts. On lower levels this pacification gets increasingly difficult as issues tend to get more concrete, technical and social functions and interests are increasingly perceived to be incompatible and compromises become less readily available (Turnhout, 2003).

Reflection

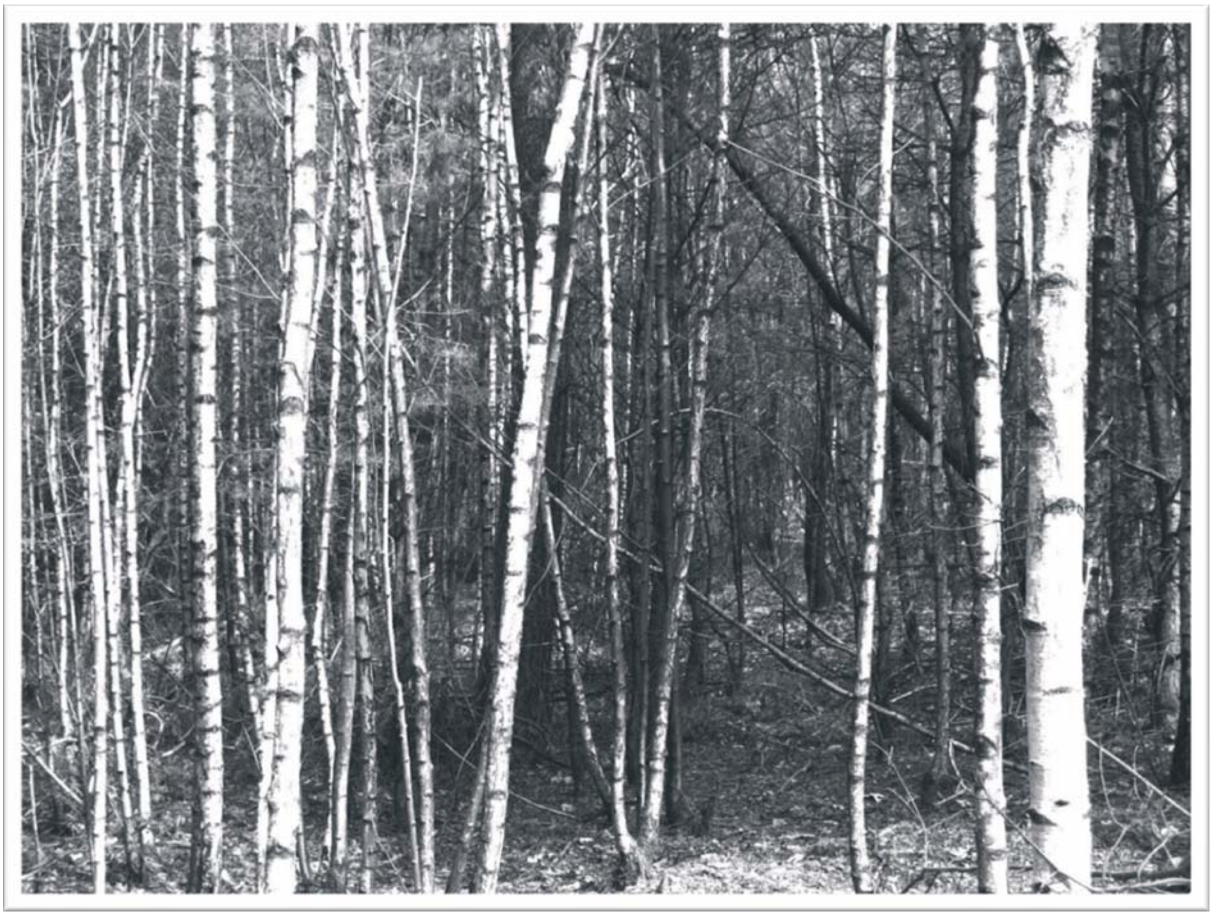
So far we have attempted to describe, characterize and compare different interpretations and meanings of EM. In this section we will consider the consequences of our findings and present our views on this.

First of all, we want to stress that diversity in interpretations and meanings of EM is not only inevitable, but also not necessarily problematic. As we have stated before, vague concepts such as EM can be inspiring and can have an important communicative function and are able to connect actors with different beliefs and interests. For example, the review by Siry et al. (2005) shows that virtually all stakeholders find sustainable forest management (SFM) a goal worth pursuing and many countries are trying to achieve SFM, and certainly try to report data that shows their orientation towards SFM goals.

However, we do worry about the dominance of technical science elements in the selected national documents. In light of sustainability, it is clear that the national level documents seem to be restricted to ecological sustainability, excluding socio-economic sustainability. We feel that this may become problematic.

Ecosystem Management —as a strong policy concept— certainly can contribute to improving forest management, but this might require a bottom-up strategy (cf. Knight & Meffe, 1997). In such a strategy, EM can provide an overall guiding objective, moving forest management towards more adaptive and ecologically-sensitive best practices. Such an approach contrasts with the top-down prescriptive approach which so far has lead to interpretations that continue traditional, nationally institutionalised management and which therefore do not fully concur with EM (cf. Knight & Meffe, 1997). A bottom-up approach emphasises a policy-based facilitation and a provision of guiding objectives, and does not exclude a diversity of approaches. Management objectives would be considered within a larger spatial, temporal and socio-political framework, i.e. expanding from the stand level to the landscape level, from goods and services to ecosystem integrity, from sustained yield to sustainable use, from operations-based to ecosystem-based management, and incorporating not just technological-scientific but also socio-political considerations.

The implicit assumption we made is that policy aims to facilitate and encourage desirable practices (cf. Grayson, 1993). These ‘practices’ are then the focus when implementing concepts like EM in policy documents. If the implementation of a political concept (like EM) changes at the times it is transported to lower levels of governance (a top-down approach), it will potentially not meet the original objectives. Therefore, regarding the implementation of EM, a different approach would be better suited (a bottom-up approach). Nevertheless, despite the inevitable diversity in the implementation of international policies, management regimes that come from a bottom-up best-practices approach (regardless of the implementation level) will have more potential to adhere to Ecosystem Management than the continuation of traditional management regimes.



CHAPTER 3

Allometric biomass equations for saplings of Silver birch, Douglas fir, Scots pine and Japanese larch

M. Dekker and J.F. Oldenburger

Introduction

Many studies that investigate scenarios of forest management depend on biomass data. Most importantly the effects of alternative management strategies on forest functions like carbon sequestration are modeled (Mohren, 2003). As biomass data are laborious to collect, however, they alternatively come from published sources, often allometric data relating a tree's biomass to its linear dimensions (e.g. DBH). Many such biomass equations already exist (Ter-Mikaelian and Korzukhin, 1997; Zianis et al., 2005; Wang, 2006) but often these sources comprise data on adult trees in even-aged stands, with many species, sizes and climatic (sub-)regions missing. With the contemporary focus on forest management systems that apply gap rejuvenation, also information on natural regeneration is important (Mosandl and Küssner, 1999). Such data on saplings and small trees exist (Geudens et al., 2004; Xiao and Ceulemans, 2004) but are nevertheless scarce. Adding to a growing biomass database, including raw data and allometric equations, therefore remains important, see for example Zianis and Mencuccini (2003) and Alberti et al. (2005).

In this paper we present biomass data and allometric equations for four tree species which are important species in the natural regeneration on dry sandy soils in the Netherlands, but which are also important timber species in Europe in general. These species are Japanese larch (*Larix kaempferi* Carr.), Scots pine (*Pinus sylvestris* L.), Silver birch (*Betula pendula* Roth.), and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco). The first three species are light demanding, the last one is comparatively shade tolerant (Mayer, 1992; Burschel and Huss, 1997). Together, these species dominate the natural regeneration in gaps in the eastern part of the Netherlands. We specifically study the rarely included size range from saplings to small trees.

Methods

Study sites

We collected data from five large gaps with a dense fully-stocked regeneration of all four species in three areas in the densely forested eastern part of the Netherlands. These areas are the *Sallandse Heuvelrug, de Hoge Veluwe* and *Schaarsbergen*. Next to our focal species there were only few individuals of other species (*Picea abies, Betula pubescens, Sorbus aucuparia, Quercus robur, Prunus padus*) present in each gap. All sites had humic to gleyic podzols with low soil water availability and nutrient content (Anonymous, 1975; Driessen and Dudal, 1991). The climate is Atlantic maritime, long-term annual temperature in the Netherlands is 9.7° C, the warmest month is August with 21.9° C on average, the coldest month is February with –0.1° C. Average annual precipitation is 771 mm, more or less equally distributed over the year (KNMI, 2005). All areas were comparable with respect to stand type and species composition.

Data collection

In winter 2002/2003 we harvested 113 whole saplings and trees and transported them to the lab for measurements on stem and branch biomass. For *Larix keampferi n*=24, for *Pinus sylvestris n*=28, for *Betula pendula n*=31, and for *Pseudotsuga menziesii n*=30, we will refer to these species by genus name only from hereon. In selecting the individuals we applied stratified random sampling in order to incorporate a relatively large range in DBH (1.6 - 137 mm), height (1.33 - 11.8 m) and crown positions (CPI; see Clark and Clark, 1992).

We first measured fresh weight for each stem. From each individual tree we then collected two stem discs and determined their fresh and dry weight. To obtain dry weight the discs were oven dried for 48 hours at 104°C. Next, a dry weight to fresh weight ratio was calculated per individual based on the two samples, and multiplied with the stem's total fresh weight. This approach is similar to (Bartelink, 1996). To determine total branch dry mass per individual tree, we first measured the diameter (3 cm from the stem) and length of all branches. Next, per individual a ten percent stratified random sample of these branches was taken, and oven dried. The sample size ranged from more than one hundred to nearly four hundred branches per species. Finally, in summer 2004 leaf biomass was sampled from a total of 64 trees (16 trees per species) in two of our gaps, i.e. a 5 and 15 year old gap. In each gap we sampled 8 trees per species. One branch was taken from the high, middle and low part of the crown, yielding a total of 192 branches. After oven drying, the needles or leaves and the branches were separated and weighed.

Data analysis

In the analysis total biomass was divided into three components which were subsampled and separately analyzed. As a result care has to be taken to ensure additivity of the components and their error terms (Parresol, 2001; Zianis and Mencuccini, 2003; Bi et al., 2004; Geudens et al., 2004), i.e. the sum of the parts must not exceed the whole. The model used in our analysis, $Y = \alpha X^{\beta} + \varepsilon$, holds when the total biomass regression function is defined as the sum of the separately calculated best regression functions of the biomass components (Parresol, 2001). In our case we separated stem, branch and foliage biomass so this translates to a three component approach with X the regressor vector and *b* the parameter vector:

$$\hat{y}_{stem} = f_1(X_1, b_1) + \varepsilon_1; \quad \hat{y}_{branch} = f_2(X_2, b_2) + \varepsilon_2;$$

$$\hat{y}_{foliage} = f_3(X_3, b_3) + \varepsilon_3; \quad \hat{y}_{total} = \hat{y}_{stem} + \hat{y}_{branch} + \hat{y}_{foliage} + \varepsilon_{total}$$

The three biomass components were analyzed in three steps. In *step 1*, stem dry mass was calculated by multiplying the dry weight to fresh weight ratio with stem fresh weight. *Step 2*. For the 10% branch subsample a weighted non-linear regression was performed using the model $Y = \alpha * d^{\beta} * l^{\gamma}$, where *Y*=branch dry mass, *d*=branch diameter and *l*=branch length. The applied weight function was d^{-3}, which homogenized the residuals. Outliers were identified and removed using diagnostic statistics according to Schabenberger and Pierce (2002). In the most extreme case this resulted in 12 branch data points removed out of a total of 399, with the R^2 increasing from 0.59 to 0.96. The number of removed outliers per species is reported in the Results section. *Step 3*. In analysing foliage mass, based on the raw data we applied a linear model for the two upper crown parts: $Y = \alpha + \beta * DM$, with *Y*=leaf dry mass and *DM*=branch dry mass. The lower crown part of the three light-demanding species however did not show such a clear relationship and we chose a saturating model: $Y = \alpha * logDM$, with *log* meaning the natural logarithm. The rationale was that the effect of cumulative branch growth combined with declining light levels down the canopy will lead to a decreasing ratio between branch mass and foliage mass in the lower parts of the crown, as is the case in this model.
In the final analysis of total tree biomass the measurements for stem dry mass, and the estimates for total branch and foliage mass were added to yield total aboveground dry mass per tree. We then regressed this on DBH using the non-linear additive model presented above. No weighted regression was performed since the data did not show heteroscedasticity.

In presenting the goodness-of-fit for the particular statistical models, for the linear models the R^2 is presented, and for the non-linear models, for which the R^2 statistic is undefined, the *pseudo* R^2 is given. This cannot be interpreted as fraction of total variance explained, but the higher its value the better the model (Schabenberger and Pierce, 2002). All analyses were done using the SAS System for Windows V8.

Results

The three biomass components: stem, branches and foliage

Betula was the species with the largest stem biomass for a given DBH, the other species were more or less undifferentiated (Fig. 3-1). Having the dry weights of all stems (step 1, data supplied as Supplementary Material), no further regression analysis was needed.

The most striking feature in the relationship between individual branch biomass and its diameter is the difference in range of both variables between species (Fig. 3-2). *Pinus* and *Betula* on the whole clearly had larger and heavier branches than did *Larix* and *Pseudotsuga*. Based on the regression coefficients (Table 3-1) and the diameters and lengths of all branches, we calculated total branch dry mass at the whole tree level (i.e. *step* 2).

There was a linear relationship between foliage mass and branch mass for the combined upper and middle crown positions for all species (Fig. 3-3). This however was not the case for the lower crown position where branches of the light-demanding species *Betula*, *Pinus* and *Larix* showed a much weaker and more variable relationship. Contrary to the light-demanding species, the shade-tolerant *Pseudotsuga* still showed a linear relationship between branch mass and foliage mass in the lower crown part. The relationship however was different between younger (5 yr) and older (15 yr) trees, which is likely related to the differing absolute canopy depth between the young and old stand, and the degree of shade needed to cause leaf mortality in this species.

The species-specific relationships between leaf and branch mass (Table 3-2) together with the branch data allowed us to calculate total foliage dry mass at the whole tree level (i.e. *step 3*).

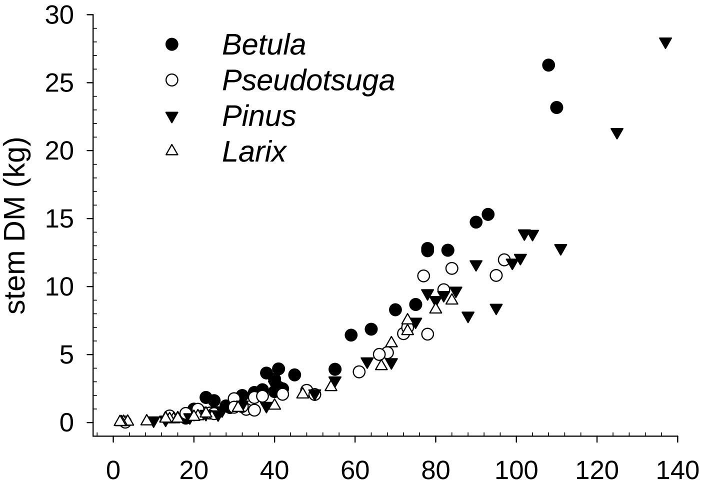


Figure 3-1. Stem biomass in relation to stem diameter. As only the raw data are used no regression lines are drawn

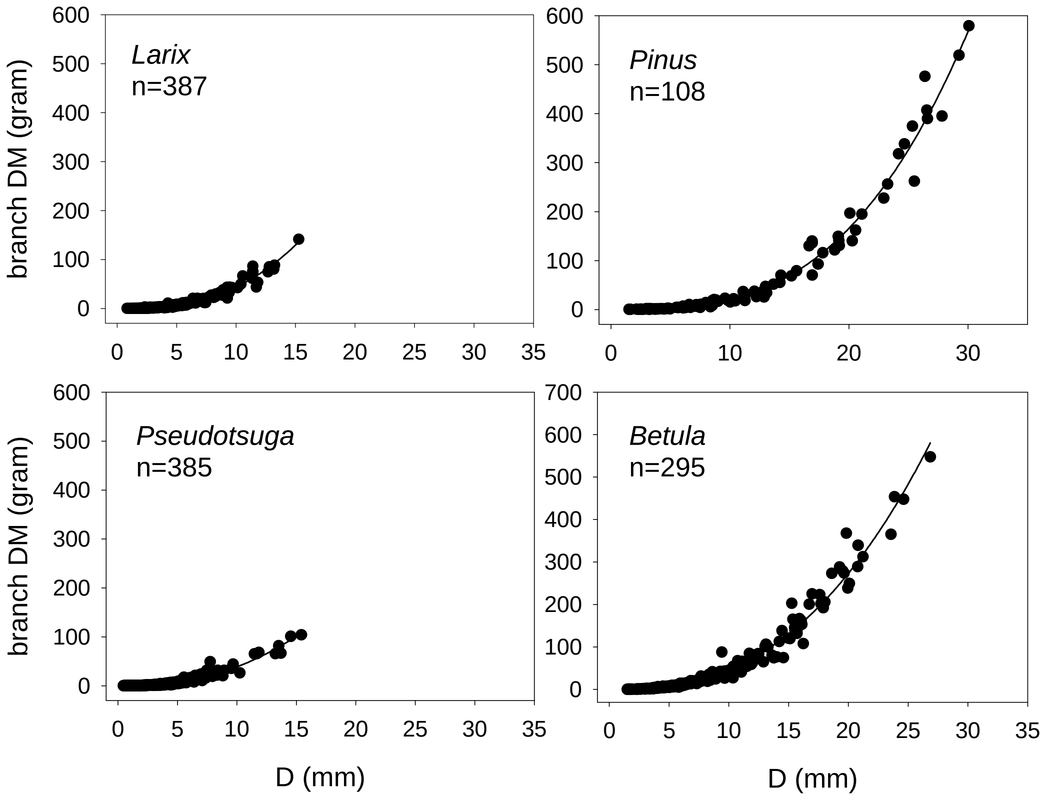


Figure 3-2. Branch dry mass (DM) in relation to branch diameter (D). For each species the number of branches is given (n), regression coefficients are described in Table 3-1

Table 3-1. Regression coefficients for the branch biomass data. Statistical model: Y = α * diameter$^{\beta}$ * length$^{\gamma}$, between brackets the standard error of the parameter estimate is given (SEE). Significance level *=0.05 **=0.01 *=0.001. For a description of the number and size range of the harvested trees, see Table 3-3**

	Larix	*Pinus*	*Pseudotsuga*	*Betula*
α	0.009(0.002)***	0.007(0.002)***	0.003(0.001)**	0.033(0.010)***
β	2.177(0.055)***	2.527(0.103)***	1.588(0.043)***	2.393(0.089)***
γ	0.704(0.061)***	0.487(0.100)***	1.166(0.047)***	0.333(0.099)***
N branches	387	108	385	295
outliers removed	12	1	0	1
Pseudo R^2	0.96	0.98	0.97	0.97

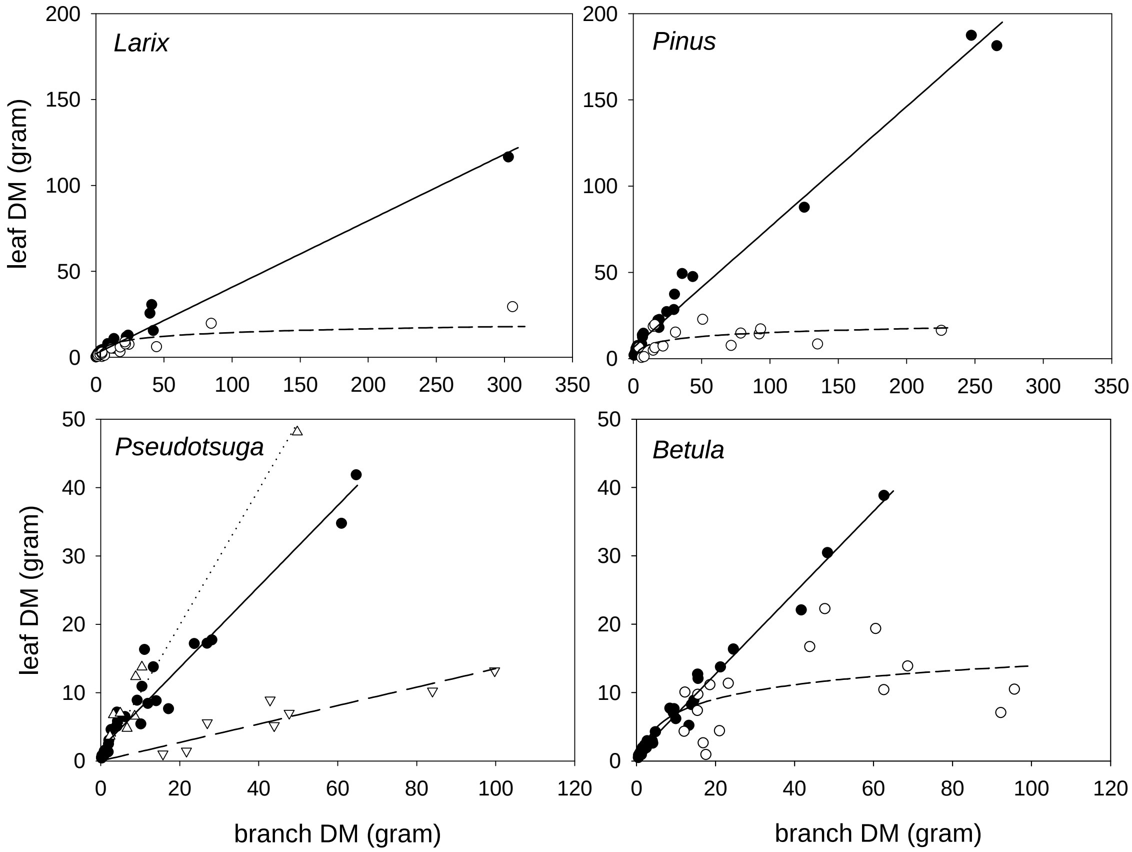


Figure 3-3. Leaf dry mass in relation to branch dry mass. The closed circles represent the data from the upper and middle crown positions (normal regression line). The open circles represent the data from the low crown position (short-dashed regression line). Alternatively, in Douglas fir, the low crown position is represented by upward triangles (young stand: dotted line) and downward triangles (old stand: long-dashed line). Note the different scales on the x- and y-axes

The whole-tree level: total aboveground biomass in relation to DBH

Adding the three biomass components from the three separate steps yielded the total aboveground biomass (Fig. 3-4). The relationship between DBH and total aboveground biomass is mainly determined by the contribution of stem mass. Similarly therefore, *Betula* has more aboveground biomass for a given DBH than do the other species, which again form a rather undifferentiated group. The regression coefficients are given in Table 3-3.

Table 3-2. Regression coefficients for the leaf biomass data and description of the dataset. DM=dry mass, log=the natural logarithm. Between brackets the standard error of the parameter estimate is given. Significance level *=0.05 **=0.01 *=0.001**

	Larix	*Pinus*	*Pseudotsuga*	*Betula*
Model 1 (high and middle crown position)^{a}	α: 2.045(0.590)** β: 0.387(0.011)***	α: 6.365(1.111)*** β: 0.699(0.016)***	α: 1.787(0.505)** β: 0.593(0.027)***	α: 0.809(0.276)** β: 0.595(0.015)***
Model 2 (low crown position)^{b}	3.112(0.401)***	3.269(0.411)***	2a: 0.992(0.051)$^{***\ c}$ 2b: 0.135(0.011)***	3.019(0.368)***
R^2 model 1	0.97	0.98	0.94	0.98
R^2 model 2	0.79	0.80	2a: 0.98 ^{c} 2b: 0.95	0.81
N branches	48	48	48	48
N trees	16	16	16	16
DBH range (mm)	2 - 129	6.5 - 107	2a: 3.8 - 21.8 ^{c} 2b: 27.0 - 86	7 - 57

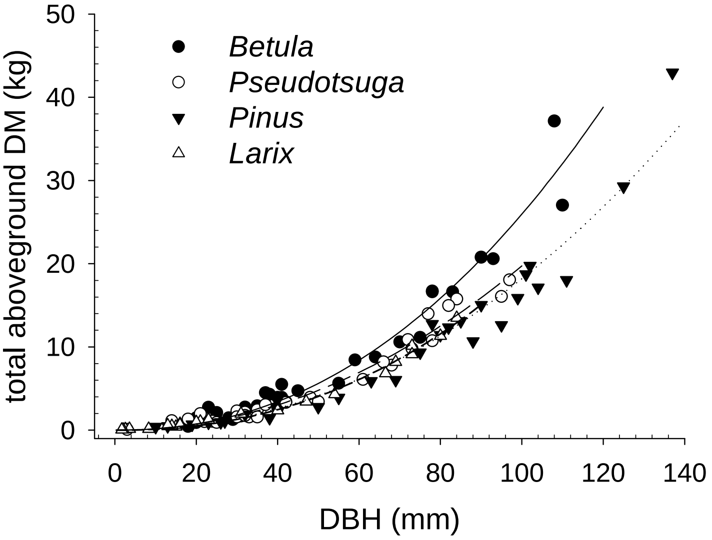


Figure 3-4. Total aboveground biomass in relation to DBH. The regression of Silver birch is represented by the normal line, Douglas fir by the long-dashed line, Scots pine by the dotted line, and Japanese larch is indicated by the short-dashed line

Table 3-3. Regression coefficients for the total aboveground biomass data and description of the dataset. Statistical model: $Y = \alpha DBH^{\gamma}$, between brackets the standard error of the parameter estimate is given. Significance level *=0.05 **=0.01 *=0.001 NS=not significant and left out**

	Larix	*Pinus*	*Pseudotsuga*	*Betula*
α	$0.653(0.281)^{*}$	NS	$1.593(0.752)^{*}$	NS
β	$2.232(0.100)^{***}$	$2.130(0.006)^{***}$	$2.047(0.108)^{***}$	$2.207(0.006)^{***}$
Pseudo R^2	0.99	0.95	0.97	0.96
N trees analysed	24	28	30	31
DBH range (mm)	1.66 - 84	10 - 137	3 - 97	18 - 110
Height range (m)	1.33 - 9.6	1.56 - 7.05	1.48 - 9.2	4 - 11.8

Discussion

In this study we (sub)sampled branch and leaf biomass in order to construct separate allometric relationships at the branch level, and subsequently estimated total branch and leaf biomass at the whole-tree level. We finally added the branch and leaf mass estimates to the stem biomass to come up with total aboveground biomass. This approach ensured the additivity of the biomass components and their error terms (Payandeh, 1981).

The logarithmically transformed data of the foliage mass in the lower crowns parts was not back transformed using a correction factor, contrary to Zianis and Mencuccini (2003). The reason is that the logarithmic model already relatively poorly described the data, having a variance much larger than any bias. As the foliage mass of the lower crown parts only contributes marginally to total aboveground biomass, this however does not distort the outcome of the final analyses. The remaining allometric relations at the branch level show the high coefficients of determination that are usual in such studies (Ter-Mikaelian and Korzukhin, 1997; Zianis et al., 2005; Wang, 2006). In general there is a strong correlation between biomass and its linear dimensions (Zianis and Mencuccini, 2004).

A different soil and climate have an effect on a species' allometry (Gilmore, 2001) and it is therefore not possible to compare all allometric studies of the same species. As a result of this, as well as methodological differences, we found only two studies that are comparable to ours in terms of soil, climate and species. Bartelink (1996) set up allometric equations for Douglas fir (*Pseudotsuga menziesii*) but he used a logarithmic transformation of the data so the resulting model cannot be directly compared to the non-linear model used in this study. Re-analysis of his data for DBH<10 cm (n=7) following our model showed that contrary to our results the α-parameter is not significant in his dataset. Therefore only a t-test for a difference in the β-exponent is

carried out. The test H_0: β_1-β_2=0; $\{(b_1-b_2) - (\beta_1-\beta_2)_{Ho} / SE(b_1-b_2)\} = 0.011/0.473 = 0.233$; $\nu = 35$; $p(t_{Ho} \geq t) = 0.409$ shows that the β's are the same.
Another study that is comparable to ours is done by Xiao and Ceulemans (2004). They set up allometric relationships for Scots pine (*Pinus sylvestris*, *n*=8) and applied the same model. Our model however does not have the significant α-parameter reported by these authors. We therefore again only carried out a t-test for a difference in the β-exponents. The test H_0: β_1-β_2=0; $\{(b_1-b_2) - (\beta_1-\beta_2)_{Ho} / SE(b_1-b_2)\} = 0.104/0.106 = 0.981$; $\nu = 34$; $p(t_{Ho} \geq t) = 0.167$ also did not yield a significant difference between the β-exponents.
Both tests showed no difference despite the fact that the data were measured on a different diameter range (less very small individuals) and on fewer trees. This did influence the α-parameter, however, the scaling exponents (β) can be said to come from the same population. These results suggest that the allometric equations presented in this study are likely to be representative for a larger area, i.e. dry and poor sandy soils under an Atlantic climate.

CHAPTER 4

Effective height development of four co-occurring species in the gap-phase regeneration of Douglas fir monocultures under nature-oriented conversion

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Introduction

The application of nature-oriented forest management is an important policy objective in Europe (MCPFE, 2000), similar to the ecosystem management concept in North-America (Christensen et al., 1996). It aims at stable, diverse and economically sound forests (Farrell et al., 2000; Führer, 2000), and incorporates natural dynamics by applying natural regeneration in canopy gaps (Bengtsson et al., 2000; Gamborg and Larsen, 2003). Likewise, under transformation management of even-aged monospecific stands gaps are created which are then naturally regenerated. The natural regeneration that follows strongly influences future forest structure as well as tree species diversity at the scale of a single gap and the whole forest (Franklin et al., 2002; Oliver and Larson, 1996; Schütz, 1999c).

The ecological and silvicultural literature suggests that different tree species occupy different positions during forest development after gap creation, ranging from pioneers that overtop all other species to shade-tolerant trees that survive in the shaded understory (Oliver and Larson, 1996; Smith et al., 1997). Alternatively, the strong asymmetric competition for light in the canopy can result in the competitive exclusion of weaker competitors for light (Canham et al., 1994; Yokozawa et al., 1996). Trees that successfully compete for light in the early gap phase grow more rapidly in height and therefore shade slower trees (Oliver and Larson, 1996). Rapid height gain however comes at a cost when it is accompanied by lower investments in radial stem growth and horizontal crown expansion (Sterck and Bongers, 1998). A high radial stem growth and slow height gain may allow trees to survive the mechanical forces (e.g. falling branches) below the main canopy. More prolific crown expansion may enable them to avoid self-shading and survive in the shade below the pioneers. Trade-off's between height gain vs. radial stem growth and/or crown expansion provide a mechanism for sharing different positions in the gap, and may thus contribute to coexistence in stable forest or plant communities (Kohyama, 1993; Silvertown, 2004). These trade-offs may be derived from across species differences in architecture (Poorter et al., 2003; Sterck et al., 2001) resulting in differences in the height gained per unit of biomass invested.

In line with forest policies in the Netherlands, monocultures of the non-indigenous Douglas fir are often under conversion to uneven-aged mixed systems, mainly by creating canopy gaps that then regenerate naturally. This initially results in a species composition dominated by only four species. We believe that to regard such natural regeneration as a synecological plant community, rather than a tended crop, is important given current forest management practices because autogenic processes such as the natural development of sapling communities in canopy gaps increasingly replace active management intervention in order to create uneven-aged and multiple-species forests (Bengtsson et al., 2000; Dorren, 2004; Gamborg and

Larsen, 2003). And even though the individual species are well known, the autogenic development of these species in an unmanaged plant community, i.e. succession, falls outside of traditional silvicultural experience.

Here we present a first, explorative study on the natural regeneration of multiple species in gaps of formerly even-aged Douglas fir forests. In this paper, we specifically look at natural sapling communities in gaps that have been created as a starting point for nature-oriented forest management. We focus on differences in height, and particularly the architectural contribution to height. We do this because tree architecture and trade-off's therein play an important role in the competition for light, and access to light is important in niche partitioning and competitive exclusion between species. This research mainly serves to map out differences in effective height growth (height gain per unit increase in size, see also King (1994) between sympatric species, and to discuss how the interspecific differences in tree architecture may contribute to competitive exclusion and stable co-existence in tree communities under nature-oriented management.
We specifically address the following issues: 1) a species' architecture determines the height gained per unit increase in biomass or DBH. Species that favor height growth over diameter growth attain higher, more exposed positions in the forest canopy; and 2) species with low height growth build a more solid architecture and invest more in a large crown. In this way, they are better suited for understory conditions with falling debris and low light levels. Finally, we discuss the results in the context of species-specific light requirements, as well as the regeneration success during the ongoing succession.

Methods

Sites and species

This paper is part of an integrated research study on the development of natural sapling communities in gaps arising from nature-oriented management of formerly pure even-aged Douglas fir forest. In this study we focus on the four most abundant species in the regeneration in such gaps: Silver birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.), Japanese larch (*Larix kaempferi* Carr.), and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco), see Table 4-1. These species dominate the species composition in gaps in Dutch Douglas fir forests in variable proportions.
Data collection was done in gaps and small clearcuts in representative stands in the eastern part of the Netherlands. Sites were selected based on the following criteria: 1) sites were residual stands of mature Douglas fir, 2) sites presented gaps occupied by all four species, 3) gaps were fully stocked, with little or no management interventions applied, 4) the regeneration covered a large range in sapling sizes, and 5) forest stands were comparable to each other in species composition and soils. This resulted in five sites in which the residual Douglas firs were 40 to 60 years old and 25 to 30 m high. Gap size

ranged from 1 to 3 times the local tree height. Species abundances varied but species composition was limited to the four focal species with only few individuals of other species (i.e. *Picea abies*, *Betula pubescens*, *Sorbus aucuparia*, *Quercus robur*, *Prunus padus*). Stem density varied within and between gaps from 0.5 to 6 individuals per square meter, in line with a large range in sapling sizes (see next section). Soils were all humic and gleyic podzols developed from cover sands from the Holocene, characterised by a low soil moisture and nutrient supply (Driessen and Dudal, 1991).

Data collection

For determining woody biomass, a total of 113 saplings and trees *i.e. Betula* (n=31), *Pseudotsuga* (n=30), *Pinus* (n=28), and *Larix* (n=24), were harvested in the size range 0.16 to 13.7 cm diameter at breast height (DBH), and 1.33 to 11.8 m height. We assume that the selected individuals present a comparable age range per species, as we harvested individuals of all four species from each individual site, and in a similar overall size range. Sampling took place in winter of 2002/2003. We applied stratified random sampling in order to sample a large range in DBH, tree heights and crown positions. For crown position we used a four point scale crown position index (CPI) ranging from 1: a suppressed position, to 2: a sub-canopy position, 3: in the main canopy, and 4: an emergent crown. Sampling over many sizes and crown positions allowed us to compare effective height development in the sapling stage. Though qualitative, CPI estimates a tree's crown position relative to its neighbors and is therefore a proxy for light availability (Clark and Clark, 1992). CPI data are able to discriminate between species' ontogenetic trajectories, and sampling over a large range therefore offers a good insight into overall species performance (Poorter et al., 2005).

Fresh weight was determined for each stem. From each individual tree we collected two stem discs (thickness ~2 cm) and both their fresh and dry weight were determined. To obtain dry weight the discs were oven dried for 48 hours at 104°C. Per individual a dry weight to fresh weight ratio was calculated based on the two samples, and multiplied with fresh weight. This approach is similar to Bartelink (1996). To determine total branch dry mass per individual tree, first the diameter (3 cm from the stem) and length of all branches were measured. Next, per tree a ten percent stratified random sample of these branches was taken, and oven dried. The sample size ranged from more than one hundred to nearly four hundred branches per species. As the trees were collected in winter, we could not sample leaf biomass. We therefore sampled leaf biomass on an additional 16 trees per species in the summer of 2004. With these data we set up species-specific leaf mass-branch mass relationships and used these to estimate total leaf mass for each of the first 113 trees. For each of the additional trees, one branch was selected and harvested for each of three crown layers, i.e. the upper, middle and lower part of the crown, yielding 192 branches. The trees in which we sampled leaf biomass matched the size range of the first 113 trees, with DBH ranging from 0.2 to 12.9 cm, and height ranging from 1.45 to 10.95 m. After oven drying the needles or leaves and the branches were weighed separately.

Additionally, we harvested 12 more individuals per species in the oldest site (~15 years old) to determine average annual growth rates. We recorded height and determined age and ring widths by counting and measuring the growth rings under an ocular micrometer. Ages ranged from 7 to 17, averaging at 12.4 years. Sizes were similar to the first 113 trees with DBH ranging from 3.1 to 8.3 cm, and height ranged from 2.5 to 9.1 m. All selected individuals were either dominant or emergent, and therefore grew under high light conditions. Given the nutrient and water limited site conditions, these trees are expected to come close to the local potential maximum growth.

Table 4-1. Characteristics of the research species (Burschel and Huss, 1997; CABI, 2005), wood densities from Wiselius (2001), Specific Leaf Areas are local values from own data (unpublished). DBH is diameter at breast height, ρ gives the wood density, Bp is *Betula pendula*, Lk is *Larix kaempferi*, Pm is *Pseudotsuga menziesii*, Ps is *Pinus sylvestris*

	lifespan (years)	**height** (m)	**DBH** (cm)	**leaf lifespan** (years)	**light demand**	**ρ** (10^2 kg m^{-3})	**SLA** (cm^{-2} g^{-1})
Bp	90-100	20-30	18-25	deciduous	Light demanding	6.73	225.6
Lk	~200	27-30	~50	deciduous	Light demanding	4.81	185.3
Pm	>600	80-100	200	5-8	Shade tolerant	5.8	78.1
Ps	>250	30-35	>50	~3	Light demanding	4.5	62.6

Data analysis

Total aboveground biomass was divided into stem, branch and leaf biomass. These were sub-sampled and separately analyzed in three steps. In *step 1*, stem dry mass was estimated from the total stem fresh weight and the individually determined fresh weight to dry weight ratio. *Step* 2. For the 10 percent branch sub-sample a weighted non-linear regression was performed using the model $Y = \alpha * d^{\beta} * l^{\gamma}$, where Y=branch dry mass, d=branch diameter and l=branch length. This is a form of the standard allometric model (Niklas, 1994; Payandeh, 1981). The applied weight function was d^{-3} which had a linear relationship with sample variance, homogenising the residuals. In order to improve the regression, outliers were identified and removed using diagnostic statistics according to Schabenberger and Pierce (2002). In the worst case this resulted in 12 branch data points removed out of a total of

399, in this example for the *Larix* data, with the R^2 increasing from 0.59 to 0.96. R^2s for *Betula*, *Pseudotsuga* and *Pinus* were 0.97, 0.97 and 0.98 respectively. With the calculated regression coefficients and the diameters and lengths of all branches, the total branch dry mass per tree could be estimated as the sum weight of all individual branches. *Step 3*. We used regression analysis to estimate the relationship between leaf biomass and branch biomass at the individual branch level. For the two upper crown parts we used a linear model: $Y = \alpha + \beta * X$, with Y=leaf dry mass and X=branch dry mass. The lower crown part of the three light-demanding species (Table 4-1) however did not show such a clear relationship and we chose a saturating model: $Y = \alpha * \log X$, with log meaning the natural logarithm. The upper, middle and lower crown part was determined from relative heights within the crown. The rationale for this approach was that the effect of cumulative branch growth, i.e. an increasing branch mass, combined with declining light levels down the canopy, i.e. a decreasing leaf mass, will lead to a decreasing foliage to branch mass ratio in the lower parts of the crown, as is the case in this model. R^2s ranged from 0.79 to 0.98 for the several models. We used these regression equations to estimate leaf biomass for each individual branch and then summed up the data to the whole tree level.
Finally we summed stem, branch and leaf mass to yield total aboveground dry mass per tree. In order to ensure the additivity of the biomass components and their error terms (see Bi et al., 2004; Geudens et al., 2004; Parresol, 2001; Zianis and Mencuccini, 2003), we defined the total biomass regression function as the sum of the separately calculated best regression functions of the biomass components (Parresol, 2001). In our case we separated stem, branch and foliage biomass so this translates to a three component approach:

$$\hat{y}_{stem} = f_1(\mathrm{X}_1, b_1)$$

$$\hat{y}_{branch} = f_2(\mathrm{X}_2, b_2)$$

$$\hat{y}_{foliage} = f_3(\mathrm{X}_3, b_3)$$

$$\hat{y}_{total} = \hat{y}_{stem} + \hat{y}_{branch} + \hat{y}_{foliage}$$

where X is the regressor vector and *b* the parameter vector. No weighted regression was performed since the data did not show heteroscedasticity. The results of these analyses together with the size range per species are presented in Table 4-2.

For this paper we subsequently explored the architectural contribution to height development. With this we mean the height gain per unit increase in size, for which we use the term effective height development. We used aboveground biomass and DBH as proxies for tree size, providing two measures of effective height development. We analyzed relationships between height as the dependent variable and biomass and DBH as independent variables using non-linear regression of the form $Y = \alpha X^{\beta}$ (Niklas, 1994). We tested for differences between species using the LSMEANS function in SAS procedure GLM. This procedure tests for differences in the estimated height for each species at the mean of all biomass (or DBH) values using the standard errors of the estimates, followed by a post-hoc Tukey test. We used crown position as a covariate to test for its effect in the analysis.

We compared the species-specific effective height development with average annual height and diameter growth rates to show the contribution of architecture relative to growth rate. For diameter growth rate we took the average ring width of the final three years since the high-light position of the selected trees is not likely to have been very different over this relatively short period. To remove ontogenetic effects with increasing size we analyzed the ring width data using an ANOVA with species and the diameter at the start of the three year period as factors. Height growth rate was calculated as the cumulative height growth divided by age. We performed an ANOVA on height with species and age as factors, thus also incorporating ontogenetic effects, and then compared species at a similar age of 7 years (the age of the youngest tree) using the LSMEANS function of SAS, significant differences were determined with a post-hoc Tukey test. These values were finally divided by 7 to arrive at the average annual height growth rate.

To explain differences in effective height development we analyzed biomass partitioning and the ontogenetic trajectory of slenderness. In analyzing biomass partitioning we used the hyperbolic regression models $Y = (\alpha * X)/(\beta + X) + \gamma * X$ for *Betula*, *Pseudotsuga*, *Larix*, and $Y = (\alpha * X)/(\beta + X)$ for *Pinus* (γ not significant), with Y=biomass fraction and X=total dry mass. Differences in biomass fractions were analyzed using an ANOVA, followed by a post-hoc Tukey test to compare species pairs. Slenderness was taken as stem slenderness: the height to diameter ratio (H/D). Average differences between species were first determined in an ANOVA. Next, we plotted the development of slenderness with increasing biomass taking an H/D ratio of 100 as a relevant reference value for saplings (King, 1986).

In presenting the goodness-of-fit for the particular statistical models, for the linear models the R^2 is presented, and for the non-linear models, for which the R^2 statistic is undefined, the *pseudo* R^2 is given. This cannot be interpreted as fraction of total variance explained, but the higher its value the better the model. Residual analysis was done to check model assumptions, outliers were identified and removed when the studentized residual was considerably bigger than 2 (Schabenberger and Pierce, 2002). All analyses were done using the SAS System for Windows V8.

Table 4-2. Size range and regression coefficients for the total aboveground biomass data. Statistical model: Biomass = αDBH^{β}, biomass in g DM and DBH in mm. Between brackets the standard error of the parameter estimate is given. Significance level *=0.05 **=0.01 *=0.001 NS=not significant and left out. Species abbreviations as in Table 4-1**

	α	β	*Pseudo* R^2	DBH range (mm)	Height range (m)
Bp	NS	$2.207(0.006)^{***}$	0.96	18 - 110	4 - 11.8
Lk	$0.653(0.281)^{*}$	$2.232(0.100)^{***}$	0.99	1.66 - 84	1.33 - 9.6
Pm	$1.593(0.752)^{*}$	$2.047(0.108)^{***}$	0.97	3 - 97	1.48 - 9.2
Ps	NS	$2.130(0.006)^{***}$	0.95	10 - 137	1.56 - 7.05

Results

Effective height development

Over the biomass range studied, *Betula* was on average tallest for a given amount of aboveground biomass, *Pseudotsuga* and *Pinus* were shortest, and *Larix* had an intermediate position (Fig. 4-1). This species ranking was maintained when height was taken as a function of DBH (Fig. 4-2). The height rank order was significant for both the height-mass and height-DBH relationship, except for a non-significant difference in the height-mass relationship between *Pinus* and *Larix* (Tukey test, see Fig. 4-1 and 4-2, tested at the average value of the log-transformed biomass and DBH data: ~4 kg dry mass and ~43 mm DBH). At smaller sizes there were no clear inter-specific differences in the height-mass relationship as intra-specific variation was very high, but with increasing size inter-specific differences became more pronounced.

Species-specific average annual height growth rates showed the same picture (Table 4-3). Height growth rate was highest for *Betula*, followed by *Larix*, then *Pinus* and finally *Pseudotsuga*. Diameter growth rates showed a different picture, and differences were small and non-significant. The non-significant differences show that *Pinus* has a diameter growth rate at least equal to *Betula* and *Larix*. But even with this similar diameter growth rate, *Pinus* is far outgrown by these species in height. These differences between diameter and height growth rates, and the agreement between their height growth rates and effective height development, clearly illustrate the contribution of tree architecture in determining (relative) tree height.

During the 2002/2003 data collection of woody biomass it was not possible to sample a large size range per species in each CPI class. Particularly *Pseudotsuga* was difficult to find in the CPI classes 3 and 4, and similarly the other species had few large individuals in CPI classes 1 and 2. Height-biomass relationships however seemed hardly affected by canopy position of the tree as height-mass slopes for exposed (CPI 3-4) versus non-exposed (CPI 1-2) trees were similar (Fig. 1). We grouped the data in order to test for an effect of canopy position and size on height. This showed that species and size had an effect on height (ANOVA on log-transformed biomass data, F=19.41 and 553.10, both $p<0.0001$), but canopy position did not (F=0.65, p=0.4204). Therefore interspecific ontogenetic differences rather than exposure seem to explain variation in relative height, at least over the size range that we studied.

Table 4-3. Growth rates and effective height development of the four species. For diameter growth rate the average ring width of the last three years is given. For average height growth rate the estimated height at age 7 is divided by 7 years. Between brackets the standard deviation is given, letters indicate significant differences at the 0.05 level. Effective height development (EHD) is given here by the regression of height on log transformed biomass ($\alpha + \beta * \log DM$), species differences are given in Fig. 4-1. Species abbreviations as in Table 4-1

	Growth rate				EHD		
	Diameter (mm y^{-1})	n	Height (m y^{-1})	n	α	β	n
Bp	1.77 (1.05) a	11	1.05 (0.06) a	12	4.84	1.79	31
Lk	1.43 (0.55) a	12	0.93 (0.08) a	11	4.14	1.82	19
Pm	1.95 (0.67) a	12	0.51 (0.07) b	11	3.25	1.77	29
Ps	1.93 (0.69) a	12	0.52 (0.06) b	12	3.81	1.70	28

Biomass partitioning

The distribution of biomass over stem, branches and leaves differed between species. In general species had relatively high leaf mass fractions and low stem mass fractions at low biomass (Fig. 4-3). After a rapid decline in leaf mass fractions and a rise in stem mass fractions with increasing biomass, all three fractions leveled off to rather stable values (dry mass > 5 kg) except for *Larix*. This strong initial change in biomass fractions in small individuals caused high variation in saplings smaller than ~5 kg dry mass (Fig. 4-3). Therefore we separately tested for differences in small (<5 kg) and larger (>5 kg) individuals across species.

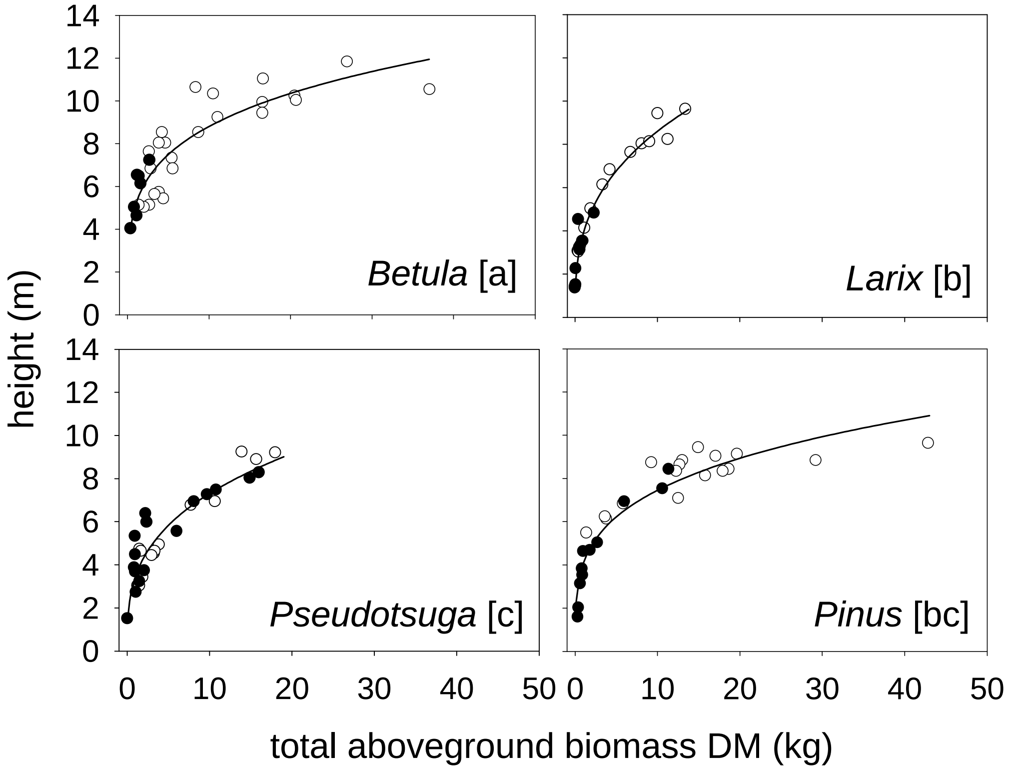

Figure 4-1. Height in relation to total aboveground dry matter. The open circles represent exposed crowns (CPI 3-4), closed circles represent crown positions ranging from the sub-canopy to suppressed individuals (CPI 1-2). Regressions are of the form H = αDM^{β}, significantly different groups at ~4 kg DM are indicated in square brackets. For *Betula* R^2=0.80, for *Larix* R^2=0.97, for *Pseudotsuga* R^2=0.86, for *Pinus* R^2=0.89

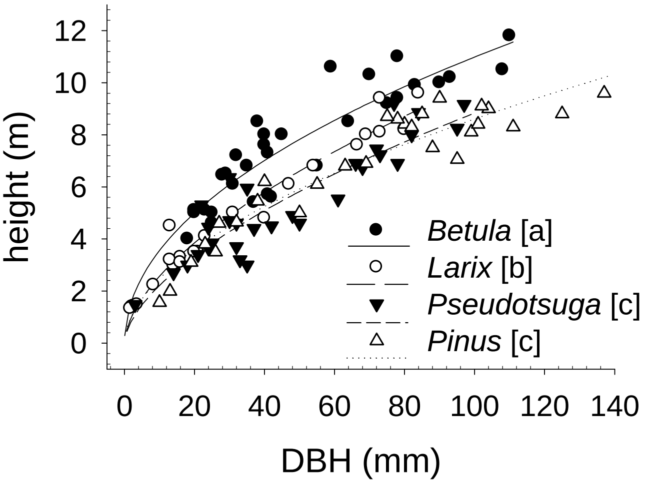

Figure 4-2. Height in relation to DBH. Regressions are of the form H = αDBH^{β}, significantly different groups at ~43 mm DBH are indicated in square brackets. For *Betula* R^2=0.83, for *Larix* R^2=0.96, for *Pseudotsuga* R^2=0.81, for *Pinus* R^2=0.90

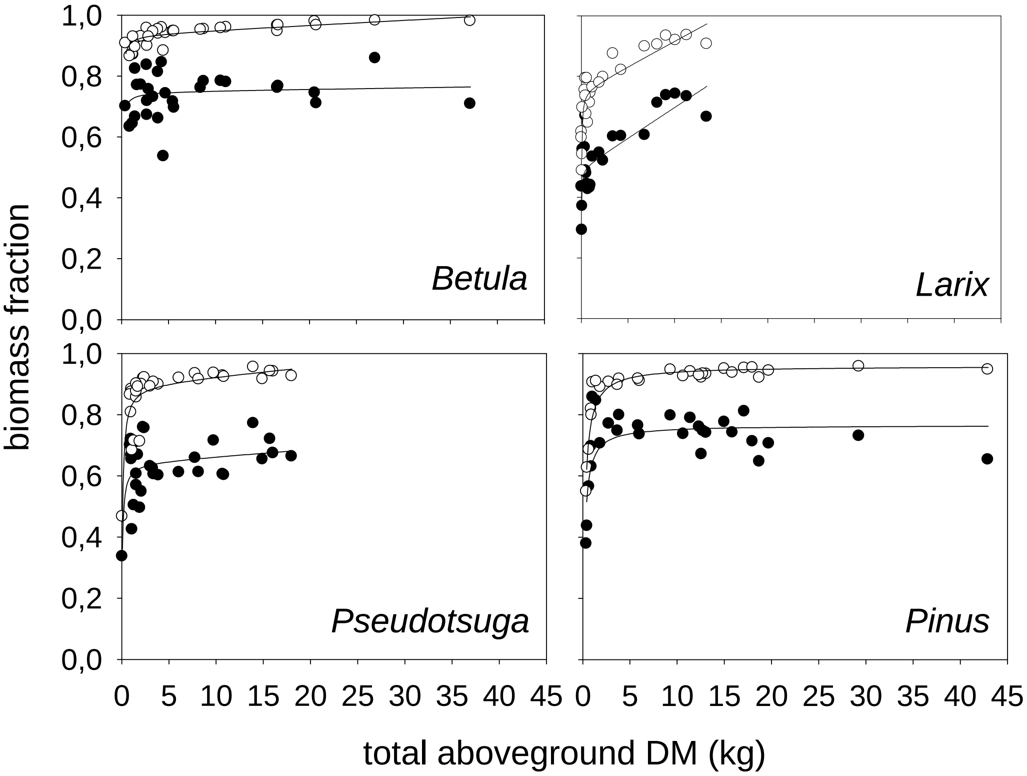

Figure 4-3. Aboveground biomass partitioning. Total tree biomass was divided into fractions for stem, branches and leaves. The closed circles represent the fraction of stem biomass (for *Betula* R^2=0.04, for *Larix* R^2=0.66, for *Pseudotsuga* R^2=0.36, and for *Pinus* R^2=0.48). The open circles represent the fraction of stem plus branch biomass (for *Betula* R^2=0.58, for *Larix* R^2=0.79, for *Pseudotsuga* R^2=0.73, and for *Pinus* R^2=0.89). The curves delineate three areas yielding the species-specific biomass partitioning: up to the first curve stem biomass is given, between curves the branch biomass is displayed, the remainder above the curves up to one is made up of leaf biomass

Stem mass fractions differed between species in both small (ANOVA, F=15.50, p<0.0001) and large individuals (ANOVA, F=8.45, p<0.001). *Larix* differed from the other species by its low stem mass fraction at small size (p<0.01), but this difference disappeared at larger size as a result of the continuously rising fractions. At larger size, *Pseudotsuga* had a lower stem mass fraction than the other species (p<0.01), though this was not significant compared to *Larix*. Regression estimates for relative stem mass at 10 kg dry mass are ~0.75 for *Betula*, ~0.66 for *Pseudotsuga*, ~0.75 for *Pinus* and ~0.70 for *Larix*.

Species also differed in the branch mass fraction in both small and larger individuals (ANOVA, F=6.01 and 6.02 respectively, both p<0.01). At greater size however, branch mass fractions became almost constant with increasing size.

Leaf mass fractions differed between species in small (ANOVA, F=13.67, p<0.0001) and large individuals (ANOVA, F=19.70, p<0.0001). The leaf mass fraction decreased with size in all species. At small size, *Betula* (p<0.0001) and *Larix* (p<0.01) had a significantly smaller leaf mass fraction than *Pseudotsuga*, *Pinus* was intermediate. At larger size, *Betula* had the smallest leaf mass fraction (p<0.0001), the other species were undifferentiated. Regression estimates for the leaf mass fraction at 10 kg dry mass were ~0.05 for *Betula*, ~0.08 for *Pseudotsuga*, ~0.06 for *Pinus* and ~0.09 for *Larix*. From Table 4-1 it can be seen that the leaf mass fractions had no clearcut correlations with Specific Leaf Area, leaf lifespan or wood density.

Slenderness

Overall, stem slenderness decreased with increasing biomass but species differed in their average H/D ratio, as can also be seen in Fig. 4-2 (ANOVA, F=11.37, p<0.0001). *Betula* and *Larix* form one group (p=0.513), *Pseudotsuga* and *Pinus* (p=0.108) another. Next to average differences species also differed in the ontogenetic trajectory of slenderness (Fig. 4-4). Across species most variation was found in small individuals (dry mass<5 kg). *Betula* gradually declined in slenderness to an H/D ratio of 100 in the biggest individuals, whereas *Pseudotsuga* maintained a ratio of 100 over the largest part of its data range. *Larix* was again intermediate between these species. Small individuals of *Pinus* were already characterized by a relatively low slenderness, while the biggest individuals showed H/D ratios of 70 and 80, the lowest of all species.

Discussion

Betula and then *Larix* gained more height per invested unit of biomass and also had the highest average annual height growth rates, and therefore overtop *Pseudotsuga* and *Pinus* in the studied sapling stage. The trees we compared were from a similar size range and grew under similar climatic and edaphic conditions. The differences we found between diameter and height growth rates, as well as the agreement between height growth rates and effective height development, show the strong contribution of tree architecture to (relative) tree height.

The lack of crown position effects on tree architecture suggests that the observed variation in tree architecture resulted from interspecific variation in plant traits rather than from phenotypic responses. Conform Osada et al. (2004), Poorter et al. (2003), Poorter and Werger (1999) and Sterck and Bongers (2001) we conclude that also in our data the phenotypic adaptation within species in sapling architecture is not as strong as the ontogenetic changes with increasing size. This agrees with other studies which report that interspecific variation in plant traits overrules phenotypic variation (Reich et al., 2003; Veneklaas and Poorter, 1998).

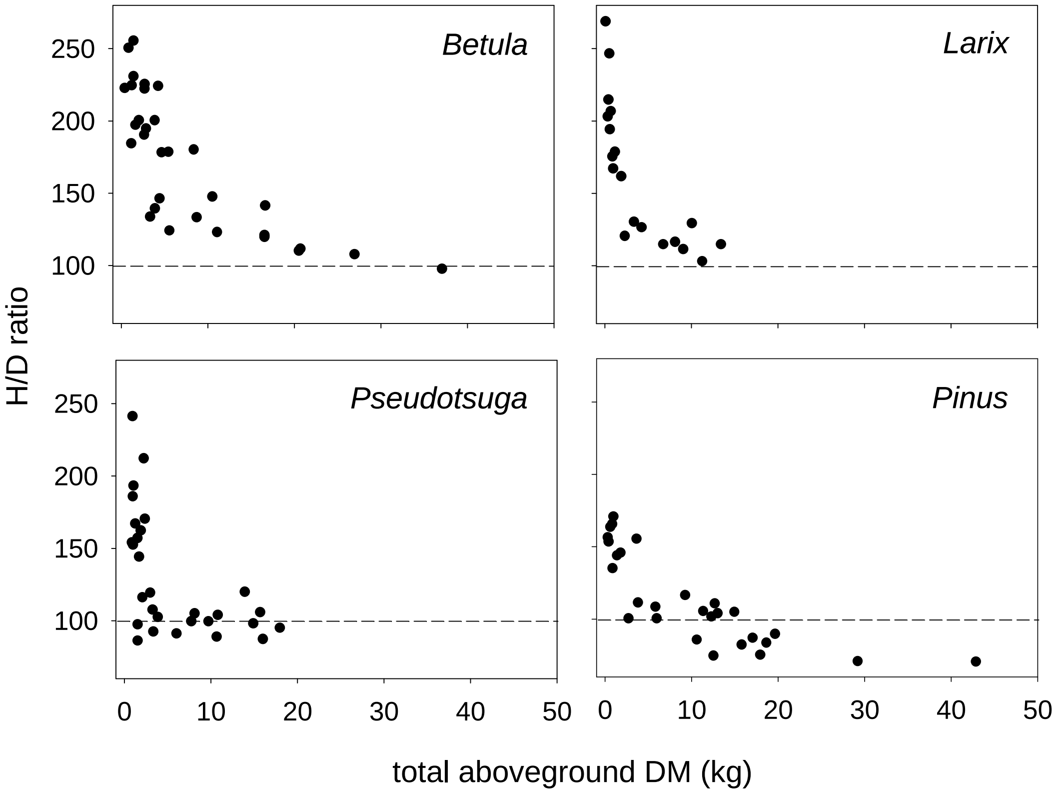

Figure 4-4. Ontogenetic development of slenderness. Reference lines are placed at a characteristic value of 100 (King, 1986)

Hence, neither phenotypic differences nor environmental variation offer an alternative explanation for our results and therefore do not confound our interpretation of the data. In the final section of the discussion we therefore explore the consequences of these interspecific differences in effective height development for competitive exclusion and stable co-existence during natural gap-phase regeneration, a key component in nature-oriented forest management.

Species differences in effective height development

The rank-order of species regarding height development with increasing biomass agreed with the rank-order determined by actual height growth rates. The tallest species for a given amount of total aboveground biomass also had the highest average annual height growth rate. Height in relation to DBH also showed clear and similar differences between species. Diameter growth rates however did not strongly diverge and actually suggested a different rank order. The correlation between the two measures of effective height development and height growth rates, and the lack of such correlation with diameter growth rates, suggest that differences in stem development contribute to interspecific differences in height growth.

These results therefore also suggest that static data on effective height development already contain information on a vertical stratification between species. The saplings we studied developed along relatively fixed height-biomass (or DBH) trajectories, that is, the variation in the height-biomass (or DBH) relationship within species was smaller than the variation between species. This is limited to the studied species and the climatic, edaphic and ecological conditions of the gap environments in Dutch Douglas fir forests. But nevertheless, as the height growth rates resulted in a similar species rank order as the analyses of effective height development, it suggests that stratification can already be deduced from static data. This results from the strong effect of tree architecture. There are likely to be differences in total carbon gain between the studied species, but given our results it is unlikely that these are big enough to result in a rank change in relative species' heights, at least in the sapling stage. This needs to be formally tested over a larger size range however.

Our results can also be used to position the studied species on the pioneer–shade tolerant axis. The pioneer–shade tolerant paradigm predicts a trade-off between effective height development and stability and/or crown expansion. As a measure for crown expansion we looked at the leaf mass fraction which, as a result of the cumulative effect of woody biomass growth over time, changes with size and/or age. The values we reported are within the range we found in literature, which varied from 1.5% for 36 year old *Betula*, to 4.5% for 33 year old *Larix*, 8.8% for on average 13 year old *Pseudotsuga*, and finally 27.6% for 10 year old *Pinus* (Bartelink, 1996; Ilomäki et al., 2003; Matyssek and Schulze, 1987; Xiao and Ceulemans, 2004). Our data represent many intermediately aged trees and their leaf biomass fractions agreed with these literature values.

Of the four studied species, only two fell predictably in line with the pioneer–shade tolerant dichotomy, the light-demanding pioneer *Betula* and the shade-tolerant climax species *Pseudotsuga*. *Betula* gained height most rapidly per invested unit of biomass as a result of its high stem biomass, high stem slenderness, and low leaf mass. It most frequently occupied exposed canopy conditions. Its low leaf mass suggests a low investment in, or high turnover of, the crown. *Pseudotsuga* took position at the other extreme with low stem biomass, low slenderness, and high leaf mass. Its high leaf mass suggests a high investment in crown expansion and/or slower crown turnover. Furthermore, *Betula* and *Pseudotsuga* are characterized by shallow and deep crowns respectively (M. Dekker, unpublished data), with deep crowns indicating an adaptation to shaded environments (Grime, 2001). These architectural parameters concur with the highest and lowest annual height growth rates of all four species.

The results for *Larix* and *Pinus* were not so straightforwardly in line with the pioneer–shade tolerant dichotomy. The pioneer *Larix* in fact displayed characteristics of both strategies. It showed an ontogenetic trajectory going from low stem mass with high leaf mass at small sizes, to high stem mass with low leaf mass at larger sizes. Comparable to *Betula* it had high stem slenderness and a high annual height growth rate. But similar to *Pseudotsuga* and contrary to *Betula* it is characterized by deep crowns (M. Dekker, unpublished data). Though *Larix* is presented as a strict pioneer in the literature (Burschel and Huss, 1997; Mayer, 1992), these results suggest a less extreme successional position for *Larix* since this species has more shade-tolerant characteristics than its pioneer status would imply. These results for *Larix* are in line with the more recent notion that pioneers and shade tolerants form a continuum rather than a strict dichotomy (Poorter et al., 2005).

The fourth species, *Pinus*, is known as a highly light-demanding pioneer (Burschel and Huss, 1997; Mayer, 1992) but had even less slender stems than the shade-tolerant *Pseudotsuga*, both at small and large size. Thus, the higher stem mass fractions of this species resulted from radial stem increment rather than from stem extension. This is supported by its relatively high diameter growth rate and low height growth rate. *Pinus*' low leaf mass fraction and shallow crowns (M. Dekker, unpublished data) suggest a small crown investment or high crown turnover. These observations contradict the idea that pioneers grow at small safety margins to successfully compete for light in the initial gap phase. *Pinus* was indeed not successful in this competition, as most *Pinus* trees were overgrown by individuals of *Betula* and *Larix*. These results show that not all pioneers consistently display a fast height growth by producing slender stems and small crowns.

Forest management implications, a hypothesis

In the Netherlands *Betula*, *Larix, Pseudotsuga* and *Pinus* co-occur as a new plant community in gaps in Douglas fir forests, brought about by gap-phase regeneration under nature-oriented forest management. A common Dutch approach to such management is to refrain from intervening in the regeneration for the first two to three decades to allow self-thinning and self-pruning to take place (Van der Jagt et al., 2000). There is however no long-term experience with this species combination, therefore the question remains what developments can be expected in that period. In this section we aim to deal with this question, though necessarily on a hypothetical basis.

For *Betula*, *Larix* and *Pseudotsuga*, our results largely confirm the pioneer–shade tolerant paradigm where pioneers grow more effectively in height, at smaller safety margins and with smaller crowns, than shade tolerants (Poorter et al., 2003). Note that intermediate species such as *Larix* may behave as shade tolerants for some characteristics while they behave as pioneers for others. Nevertheless, based on their architectural properties and their growth rates, these species are expected to partition the light in the gap environment, allowing them to coexist at least until first thinning. Given however that *Pinus* needs high-light conditions for growth and survival while its architecture and height growth rate indicate that it will be overtopped, it is not likely that this species will survive during the ongoing succession in these canopy gaps. We hypothesize that the architectural contrasts of this species, in particular its tendency to produce stout stem at the cost of height extension, disable it to compete during succession in gaps following nature-oriented management: it looses the competition for light and at the same time cannot persist in the shade. As stands of different species are intimately mixed at the landscape level in the Netherlands, *Pinus* is able to regenerate abundantly, but it is doubtful whether it can persist together with more competitive species under autogenic stand development until first thinning.

Our hypothesis is supported by the fact that *Pinus sylvestris* originates from primary succession environments as suggested by its role as a coloniser, invading Europe during the Holocene. *Pinus* also persists under harsh drought or otherwise stressed environments (Mayer, 1992). In environments that are more competitive for light, such as closed mixed forests, *Pinus* was historically often competitively excluded (Mayer, 1992; Richardson and Rundel, 1998).

From this we predict that *Pinus* will tend to be competitively displaced from this particular plant community, especially where it grows in intimate mixture with the other species. Alternatively, if local management objectives require this species to be maintained, it will require liberation from competition. Another possible way out from competitive exclusion could be to locally survive in clumps of conspecifics.

CHAPTER 5

Target species identity is more important than neighbour species identity

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Introduction

After gap formation trees establish from seed or resprouting and, together with advance regeneration, start to compete for the available growing space. After the canopy closes, competition intensifies between all individuals as they enter the stem exclusion phase, leading to high mortality and thus self-thinning (see Oliver and Larson, 1996). The strong correlation between the level of mortality and crown geometry (Lonsdale and Watkinson, 1983; Weller, 1987; Franco and Kelly, 1998) shows that the reduction in individuals and/or species at this point is mainly driven by the competition for light.
Light capture is strongly determined by leaf display (Sterck et al., 2003; Poorter et al., 2005). As light travels down the canopy, it passes through successive leaf layers and is attenuated exponentially depending on the leaf area index and leaf characteristics (Kropff and Van Laar, 1993). This reduces the amount of light available to lower-positioned leaves within the same or neighboring canopy. The ability of a tree to reduce light to a level where other individuals cannot maintain their foliage is an example of competitive pressure (Horn, 1971). Such asymmetric, pre-emptive competition (Schwinning and Weiner, 1998; Weigelt and Jolliffe, 2003) leads to leaf, and ultimately whole-plant, mortality (Givnish, 1988). Consequently, differences in light capture and attenuation between crowns of different species result in different competitive abilities (Goldberg and Barton, 1992), potentially affecting succession and species composition (Küppers, 1989; Canham et al., 1994; Yokozawa et al., 1996).

The competition for light during self-thinning is strongly influenced by tree architecture (Franco and Kelly, 1998). Tree architecture determines size-differentiation and stratification (Puettmann et al., 1992), and is an important factor in gaining canopy access in order to capture light (Poorter et al., 2003; Sterck et al., 2005). Vertical stratification between species already starts in the sapling stage (Dekker et al., 2007). Next to architecture, shade-tolerant saplings are often found to have a larger leaf area ratio and leaf mass fraction in low light compared to light-demanding species (Lusk, 2004; Lusk and Piper, 2007). Variation between species in light demand and architecture can therefore give rise to differences in biomass distribution and tree shape. This subsequently leads to a between-species variation in crown characteristics like biomass packing and crown shape, affecting light capture and light attenuation, and ultimately self-thinning (Lonsdale and Watkinson, 1983). Crown volume packing for example, i.e. the amount of biomass packed in a unit of crown volume, may be positively related to shade-tolerance, with a higher volume packing leading to stronger self-thinning (Lonsdale and Watkinson, 1983; Osawa and Allen, 1993; Osawa, 1995). Plant geometry in general is reported to play an important role in dense self-thinning stands (Lonsdale and Watkinson, 1983; Weller, 1987; Ellison, 1989), which suggests that between-species differences in crown traits and architectural make-up can affect a species' growth and survival (Sterck et al., 2003).

From the previous review we identified two important factors in the competition for light: 1) the ability to overtop resulting from a faster height growth, and 2) the ability to capture most of the incident light by displaying a large leaf mass per unit crown volume. Both factors may play an important role in a competitive light-limited situation. The question is, however, whether and how these two factors interact and determine interspecific competition, and ultimately competitive exclusion. To answer these questions we investigated the competition for light in a young and dense mixed-species temperate forest stand in the early stem exclusion phase. In this stand developmental phase, the most limiting factor is light, and density-dependent mortality outweighs mortality by other causes. Our main research questions are: a) do species vertically stratify according to light demand and/or foliage density, and b) does a higher foliage mass density, through increased light attenuation, result in a stronger competitive pressure? From such basic plant traits we aim to infer consequences for stand development.

Where most research on self-thinning is focused on even-aged single-species stands, we focus on natural mixed-species stands consisting of fast-growing pioneers and shade-tolerant species, including native and non-native species. In answering the research questions we looked at vertical stratification, differences in foliage mass density between pioneers and shade-tolerant species, and how foliage mass density affects neighboring trees. We hypothesized that a) shade-tolerant species invest more in a large crown and, given their lower leaf light-compensation point, maintain a higher foliage mass density than do light demanders that invest more in height growth; and b) that through the increased light attenuation caused by a higher foliage mass density, species with high densities exert a stronger competitive pressure than do species of low density.

Materials and Methods

Site and species

Field measurements were done in two large gaps in even-aged Douglas fir forest in the Hoge Veluwe National Park in the Netherlands. These sites are part of a larger research effort investigating the nature-oriented conversion of monospecific coniferous forests. The first site (52°2'3"N, 5°51'11"E) is a 15 year old gap of 1.2 ha, the second site (52°2'28"N, 5°50'46"E) is a 5 year old gap of 1.3 ha, comparable to the first site in species composition. The first site was created by a storm, cleared from debris, and followed by salvage cutting. The second site was created by clearcutting. We included a younger and an older community to sample a large range in tree sizes and ages, allowing us to distinguish the effect of ontogeny from species effects. We sampled only two sites since previous research (Dekker et al., 2007) showed that species-specific growth patterns (i.e. height, diameter and dry mass accumulation) in this size range are robust against site variation. Their work shows that even when the four studied species are sampled over a large area and size range, the environmental flexibility within species is less strong than the average morphological differences between species. This result was based on aboveground biomass measurements on 177 trees up to ~14 cm DBH and ~12 m height from 5 sites under similar climatic and edaphic conditions. So even though including more sites of different ages would raise resolution and statistical power, it would unlikely have an influence on the stratification or competitive effects as analyzed in this study.

Both sites are situated on humic podzol soils of coarse sand with low water holding capacity and nutrient content (Anonymous, 1975). Long-term annual temperature at the nearest weather station is 9.4° C, the warmest month is July with 17.2° C on average, the coldest is February with –0.6° C. Average annual precipitation is 860 mm, more or less equally distributed over the year (KNMI, 2005).

Both gaps contained naturally established Silver birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.), Japanese larch (*Larix kaempferi* Carr.), and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco). We selected gaps with these species for two reasons: i) their low tree species richness reduces the number of species interactions to be accounted for, and ii) these species represent a range in juvenile shade tolerance in which *B. pendula* and *P. sylvestris* are extreme pioneers, *L. kaempferi* is intermediate, and *P. menziesii* is comparatively shade-tolerant (Mayer, 1992; Burschel and Huss, 1997; CABI, 2005). This ranking of species in terms of shade tolerance is not physiologically or otherwise quantified, but is based on decades of observed responses in forest management in Western Europe. As a general ranking it provides us with a framework to evaluate broad patterns in our data.

Data collection

Ontogenetic and competitive effects

To quantify ontogenetic changes and competitive interactions between species, we measured tree pairs in both the 5-yr and 15-yr community. We selected 100 tree pairs (i.e. two adjoining trees) in the 15-yr community, and 79 tree pairs in the 5-yr community. We looked for tree pairs in all possible species combinations. Within each species combination we selected tree pairs that were characterized by physical crown contact, and in which the target tree had a specified crown position relative to the neighbor tree. This ranged from being fully overtopped by– to fully overtopping the neighbor as indicated by 1: the target tree is fully overtopped, with the crown base of the neighbor and crown top of the target tree however still in physical contact, to 2: the target tree has an inferior position to the neighbor tree, but is not fully overtopped and crowns are partly mingled, 3: the target tree and neighbor tree are at equal height, no one overtops the other, 4: the target tree has a superior position to the neighbor tree, the reverse from the second situation, and 5: the target tree fully overtops the neighbor tree, the reverse from the first situation.

We aimed for an even distribution of the number of selected tree pairs over all species combinations and relative crown positions. Tree pair selection could not be completely random, but instead selection was done by taking a random-walk approach: a direction was randomly selected and followed until we reached the gap edge, from where we started again. While traversing the gap, tree pairs were chosen when they matched our requirements on species and relative sizes, and where not within 7.5 m of remaining overstory trees. Measured trees ranged in height from 1.35 to 12.05 m.

Every selected tree pair was divided in a target tree and a neighbor tree in such a way that in the end all species and size combinations were included. On the target tree, assigned as the tree experiencing competition, we recorded species, height, DBH (diameter at breast height, i.e. 1.30 m), and crown depth. To arrive at crown depth, the crown base was defined as the height of the lowest leaf in a tree crown that is attached to a branch below which no two consecutive whorls (or major branches) are still alive, and at least two consecutive whorls (or major branches) are dead (Mäkelä and Vanninen, 1998). Crown depth is then the difference between tree height and crown base.

On the neighbor tree, consequently assigned as the tree exerting competitive pressure, we recorded species, height, DBH, crown depth, and crown width. For the neighbor tree, using the data on crown depth and crown width, we determined crown volume and foliage density (see last section of Data Collection).

In measuring competitive interactions between individuals we took relative crown depth (RCD, or crown ratio, i.e. crown depth divided by tree height) as the response variable as it is fully dependent on the presence of living leaves and thus directly responsive to the competition for light. Although water and nutrients are also limiting and subject to competition, the competition for light is the strongest factor driving leaf and branch mortality in low crown parts in dense self-thinning stands (Oliver and Larson, 1996). Studying tree pairs simplifies the fact that a tree experiences competition from all surrounding individuals. Nevertheless, a shading effect from a tree nearby will be stronger than a shading effect of a tree further away (Zeide, 2002; Canham et al., 2004). To ensure that any response in the data is the result of the interaction between these two trees, we selected trees characterized by physical crown contact and we measured crown depth along the line connecting the two trees. In this way any response in RCD is the integrated result of the whole crowns of these two trees (i.e. a self-shading and a neighbor effect) and their relative crown positions (see Data Analysis for the competition index that quantifies this last aspect). Furthermore, a competitive effect experienced by an individual target tree at this specific point, is then mainly the result of the light capture of a specific neighbor tree, excluding other density-dependent effects (e.g. Janzen-

Connell effects, see Hubbell et al., 2001). The effect of other more distant competitors will appear as noise around this signal.

Species and community characteristics
The 5-yr community was quite homogenous and individuals mostly grew in open growth conditions with little morphological differentiation within and between species. Since we were mainly interested in the differentiation in species morphology that occurs in older saplings, the 5-yr community required a smaller sampling effort to quantify morphological characteristics. We therefore economically re-used the tree-pair data on height and DBH. To prevent autocorrelations we used only the data from the appointed neighbor tree. These data contain the full range of sizes and crown positions and allow for an analysis of morphological characteristics. However, as the data are collected based on conditional sampling they cannot be used to quantify gap composition. Applying this additional selection criterion left us with a total of 79 individuals.

In the structurally complex 15-yr community a larger sampling effort was required. We therefore made use of data from a synchronous parallel study (M. Dekker and W. Veefkind, unpublished data). This study inventoried the 15-yr gap by digitally mapping out the gap circumference and the remaining mature trees, and by randomly placing 36 circular sample plots of 1.25 m radius (4.9 m^2) inside the gap, using a software routine in Mathematica. In the selection of plot locations, overstory trees were avoided by maintaining a safe limit of 7.5 m to the gap edge or remaining trees within the gap. As *L. kaempferi* occurred in low numbers in these random sample plots, we made additional measurements were it was locally more abundant.

In the sample plots additional characteristics were recorded to quantify the stand's structural complexity after 15 years of morphological differentiation and competition. The dataset contained density, species, height, DBH, crown depth, canopy position and crown class. Canopy position estimates access to light and was recorded as an index (CPI, crown position index) in five classes varying from 1: the tree does not receive direct light, to 2: it receives direct lateral light, 3: it receives direct overhead light on part of the crown, 4: it receives full overhead light on the whole crown, and 5: it has an emergent crown that receives light from all directions (Clark and Clark, 1992). Crown class records dominance versus suppression and was recorded on a four point scale (Oliver and Larson, 1996) ranging from 1: a dominant tree with a large and emergent crown, to 2: a co-dominant tree which occupies a position in the main canopy but which is restricted from the side, 3: an intermediate tree which is below the main canopy but not suppressed, and 4: a suppressed tree which is overtopped and shows signs of deterioration (i.e. small defoliated crowns, many dead branches). We recorded both CPI and crown class because CPI values only indicate the level of exposure to direct light where crown class additionally gives an estimate of a tree's vigor through its level of dominance or suppression.

Finally, to be able to interpret our data in terms of species' stratification, we harvested 30 individuals per species over all canopy position classes (6 individuals per CPI class, independent of the random sample plots). This allowed us to evaluate whether species differed in establishment time, affecting average tree heights. For this we recorded height and DBH, stem discs were taken at ground level, and ages were determined by counting growth rings on 2 radii using a Leica stereoscope.

Crown volume and foliage density

We took foliage density as foliage mass divided by crown volume. To determine foliage mass we applied allometric equations that were developed by Dekker et al. (2007). These equations are based on biomass measurements on a total of 177 saplings and small trees in the size range of 1.33 m to 11.8 m in height. Foliage mass was estimated for each branch depending on its relative position in the crown using species-specific regression estimates. These branch-level values were then summed to a total per tree. As trees in this developmental phase do not yet fully overtop one another CPI had no significant effect at the 0.05 level on these leaf mass-branch mass relations after relative branch position was accounted for. R^2 values for these branch level regressions ranged from 0.79 (lower branches of *L. kaempferi*) to 0.98 (top branches of *B. pendula*). The R^2 values for the total foliage biomass equations (in relation to DBH) are 0.73 for *B. pendula*, 0.79 for *P. sylvestris*, 0.76 for *P. menziesii*, and 0.90 for *L. Kaempferi*. The data were collected on similar sites as the present study.

We determined crown volume for each neighbor tree by using the data on both crown depth and crown width. Crown width was measured at two sides (on the imaginary line connecting the two trees) at five equidistant positions in the crown, which divided the crown into eight sections (Fig. 5-1). When taking the lower and upper section-widths as radii and assuming similarity in all directions, each section is either a cone, a conical frustrum, or a cylinder. Its volume (*V*) can then be calculated by:

$$V = \tfrac{1}{3} * \pi * h * (r_1^2 + r_2^2 + r_1 * r_2)$$

This volume was divided by two since the volume of each section only applies to one side of the tree. Adding up the volumes of all eight sections finally gives an estimate of total crown volume. We then divided foliage mass by crown volume to obtain foliage density (in g m^{-3}).

Data analysis

We analyzed the data in three blocks: species and community characteristics, ontogenetic effects, and competitive effects. These three blocks finally allow us to construct the answer to the research questions regarding vertical stratification and competitive pressure.

Species and community characteristics
Species composition in the 15-yr community was determined as the percentage occurrence in the sample plots, and stem density was quantified by dividing the number of individuals by the sample plot surface. For both communities we then examined the range in DBH and height, and to quantify species' differences in the height-diameter relationship (slenderness) we used the following regression models:

$$\text{height} = \alpha + \beta * \text{DBH} + e \qquad \text{(5-yr community)}$$
$$\text{height} = \alpha \text{DBH}^{\beta} + e \qquad \text{(15-yr community)}$$

in which α and β are regression parameters and e is the residual error term. Interspecific differences, were determined by covariance analysis (ANCOVA) including the extra measurements on *L. kaempferi*. In this analysis we additionally used crown position as a covariate.
For the 15-yr community we analyzed the effect of age (i.e. establishment time) on tree height using an ANOVA with species and DBH as covariates, and age as a factor nested within species to allow for between-species differences in establishment time. We did not transform the data as the residual plots showed that error terms were homogenously distributed. Crown class and CPI were analyzed by calculating their frequency distribution. Finally, average CPIs were determined per species to investigate vertical stratification.

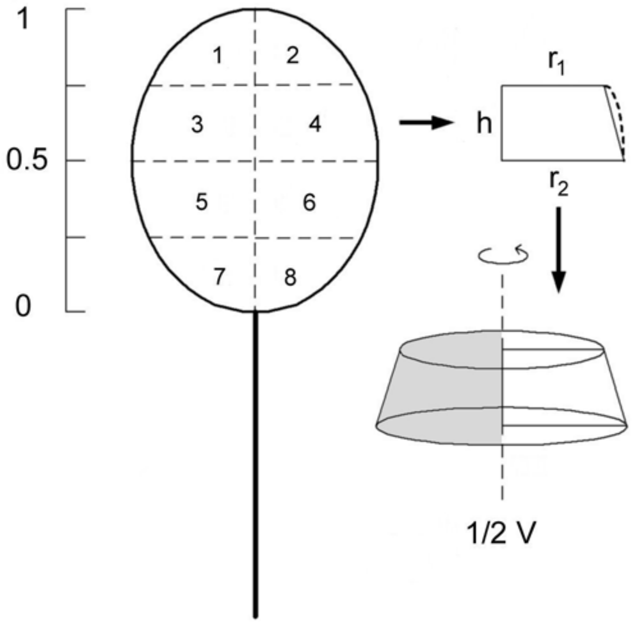

Figure 5-1. Approach used to measure crown widths and crown volume. Numbers refer to the different sections of the living crown for which volume was estimated

Ontogenetic effects

We calculated RCD as the ratio between crown depth and total tree height. We then checked for an ontogenetic effect of size (DBH) on RCD using linear regression. Additionally, we analyzed the species-specific ontogeny of crown volume in a weighted ANOVA, using DBH^{-1} to correct for heteroscedasticity. Tukey-Kramer post-hoc tests were performed to see whether RCD or crown volume were different between species. We log-transformed the foliage density data to stabilize variances as well as linearize the relationship, which we then analyzed using linear regression. We subsequently tested for differences in intercept and slope in an ANOVA using dummy variables.

Competitive effects

To correct for size differences between trees that confound species effects, we included a competition index. We calculated this competition index as the crown surface area of the neighbor tree above 66% of the target tree's height ($\mathrm{CSA}_{0.66}$ in m^2, from Biging and Dobbertin, 1995). $\mathrm{CSA}_{0.66}$ is determined by differences in crown size as well as tree height, therefore incorporating differences in canopy position, and has a strong influence on competition (Biging and Dobbertin, 1995). Crown surface area (CSA) is determined by first calculating the mantel surface (MS_i) of each of the eight crown sections according to:

$$MS_i = \pi * (r_1 + r_2) * \sqrt{(r_1 + r_2)^2 + h^2}$$

CSA was subsequently calculated as the sum of the section mantel surfaces, again halving the MS_i values since the surface of each section only applies to one side of the tree.

We analyzed competitive effects on the response variable RCD in an ANOVA using the qualitative variables target tree species and neighbor tree species, and the quantitative variables DBH and $\mathrm{CSA}_{0.66}$. The variable target tree species determines whether there is a species-specific response in the RCD, the variable neighbor tree species determines whether there is a competition-based species effect. DBH accounts for possible ontogenetic effects, the competition index $\mathrm{CSA}_{0.66}$ accounts for size differences. Additionally, as crown size might depend on species, the two interaction-terms between $\mathrm{CSA}_{0.66}$ and target as well as neighbor species are included to look at species-specific effects. We performed a Tukey-Kramer post-hoc test to see whether the effect on RCD differs between neighbor species. In two separate ANOVAs we determined whether species-specific foliage densities affect the RCD, the qualitative variable neighbor tree species is quantified by replacing it by the estimates of foliage density (g m^{-3}) and total foliage mass (g).

Statistical analyses

All statistical analyses were done with the SAS System V8. The data are grouped in four datasets: 1) the sample plot data from the 15-yr community together with the neighbor tree data from the 5-yr community; 2) the same data as in 1, but including the additional measurements on *L. kaempferi*; 3) the age data from the 120 stem discs; and 4) the tree pair data from both communities. As the distinction is important for statistical inference, we report for each analysis the applied dataset. In cases where we log-transform data, the natural logarithm is used. Residual analysis was done to check model assumptions. In presenting the goodness-of-fit for the particular statistical models, for the linear models the R^2 is presented, and for the non-linear models, for which the R^2 statistic is undefined, the *pseudo* R^2 is given. This cannot be interpreted as fraction of total variance explained, but the higher its value the better the model (Schabenberger and Pierce, 2002).

Results

Species and community characteristics

Species characteristics

Species differences in slenderness were already manifest in the 5-yr community, and became stronger in the 15-yr community (Fig. 5-2). Overall, stem slenderness differed strongest between *B. pendula* and *L. kaempferi* on the one hand, and *P. menziesii* and *P. sylvestris* on the other. In the 5-yr community *B. pendula* and *L. kaempferi* almost differed (dataset 2, ANCOVA, $p=0.052$), whereas *P. menziesii* and *P. sylvestris* clearly did not differ ($p=0.421$). These two groups, however, deviated strongly from each other ($p<0.0001$) with stems of *P. menziesii* and *P. sylvestris* on average being shorter and thicker.

In the 15-yr community slenderness was significantly different between all species after log-transformation ($p<0.05$). However, Figure 5-2B shows that *P. menziesii* and *P. sylvestris* on average attain a similar height for a given DBH, whereas *L. kaempferi* and especially *B. pendula* on average are taller.

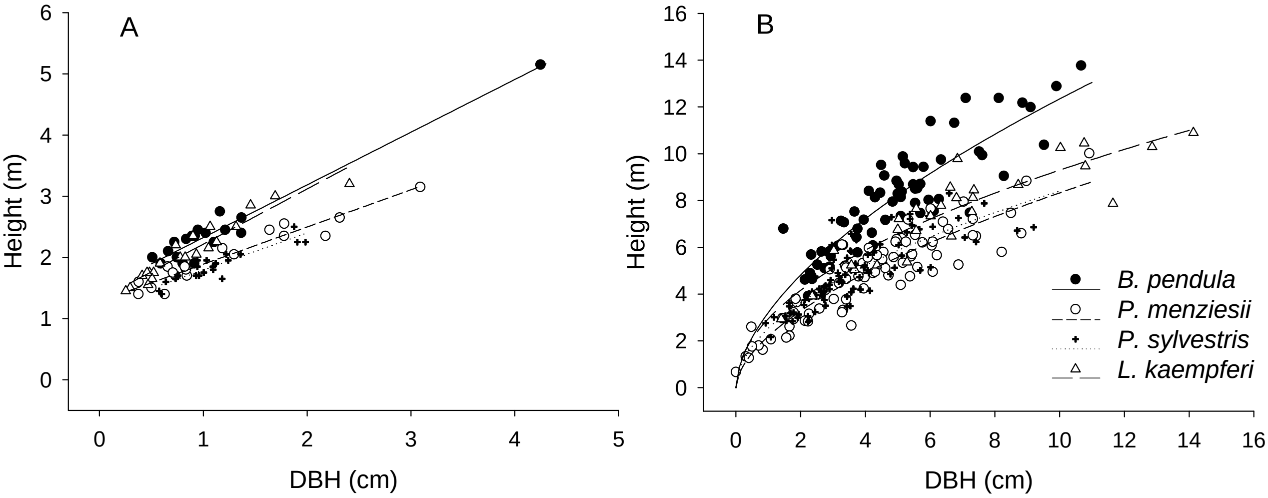

Figure 5-2. Tree height in relation to diameter for the 5 year (A) and 15 year old (B) communities. The model in A is height=$\alpha+\beta$*DBH with for *B. pendula* n=18, R^2=0.95; for *P. menziesii* n=18, R^2=0.93; for *P. sylvestris* n=22, R^2=0.83; for *L. kaempferi* n=21, R^2=0.92. The model in B is height=αDBH^β with for *B. pendula* n=64, (*pseudo-*) R^2=0.78; for *P. menziesii* n=77, R^2=0.83; for *P. sylvestris* n=92, R^2=0.70; for *L. kaempferi* n=27, R^2=0.82

Community characteristics

In the 5-yr community open growth conditions prevailed and species' heights were not much differentiated. Of all measured heights, 90% lay between 1.4 and 2.8 m height. This range, however, represents local minimum and maximum, rather than average, sizes as it is the result of actively looking for differently sized individuals in this homogenous community. We were unable to determine stem density, but species composition was similar to the 15-yr community (personal observation).

Stand structure was more complex in the 15-yr community. Total stem density in the 15-yr community was 13,747 (±898 s.e., dataset 1) individuals per hectare. Species composition varied within the gap. Only one sample plot contained one species, twelve plots had two species, twenty plots had three species, and three plots contained all four species. Overall the community is therefore intimately mixed, but areas occur which are dominated by one or two species. Stem densities ranged from 0.6 to 2.9 individuals m^{-2} in the sample plots. As plot density is related to average tree height in the plots (dataset 1, Pearson's r -0.54, $p<0.001$), this shows that dense and low patches occur next to tall and open patches.

There was large variation in diameters and heights both between and within species (see Fig. 5-2B). The average CPIs furthermore suggest a vertical stratification between species. *B. pendula* and *L. kaempferi* had an average CPI of 3.5 and 3.7 respectively (dataset 2, not different at p=0.526), whereas *P. menziesii* and *P. sylvestris* had an average CPI of 2.7 and 2.3 (both different from all other species, $p<0.05$). This vertical separation more or less followed the species ranking in slenderness (see Fig. 5-2), and was not influenced by differences in establishment time as age was not a significant factor in explaining tree heights (dataset 3, ANOVA, p=0.169). Most individuals in the 15-yr community (>80%) are between 9 and 14 years old, the median age being 12 years.

Across species many individuals receive at least some overhead light (CPI ≥ 3), but receiving only lateral light (CPI 2) is more common in *P. menziesii* and *P. sylvestris* (Fig. 5-3). The crown class data additionally show that contrary to *P. menziesii*, individuals of *P. sylvestris* are more often suppressed with signs of deterioration. The CPI of a tree did not have a significant influence on its height (p=0.175), tree height was only related to DBH and species (dataset 2, ANOVA, both p<0.0001).

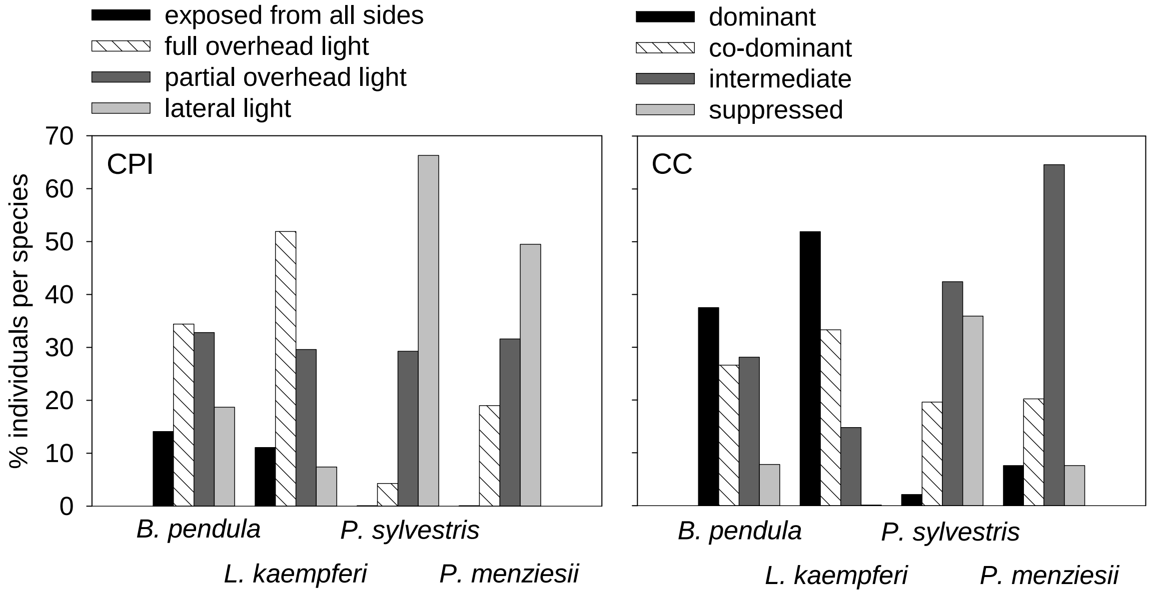

Figure 5-3. Distributions of Crown Position Index (CPI) and Crown Class (CC) in the 15-yr community. Bars represent for each species the percentage of individuals per canopy position or crown class

Ontogenetic effects

Relative crown depth

RCD tended to increase slightly with DBH in the 15-yr community (dataset 4, linear regression across species, p<0.0001), and was on average different between species. Least squares estimates (at average DBH) for RCD showed that *B. pendula* (0.38) and *P. sylvestris* (0.41) have a lower RCD compared to *L. kaempferi* (0.51) and *P. menziesii* (0.61). The RCDs of *B. pendula* and *P. sylvestris* were not significantly different (p=0.295), all others were different (p<0.01). More importantly however, trees in the 5-yr community had a higher RCD than in the 15-yr community. This difference was significant for *B. pendula* (p<0.0001), *P. sylvestris* and *L. kaempferi* (p<0.01), but not for *P. menziesii* (p=0.347). In order to separate this ontogenetic effect from a competitive effect, it needs to be incorporated as a covariate in the analysis of competition.

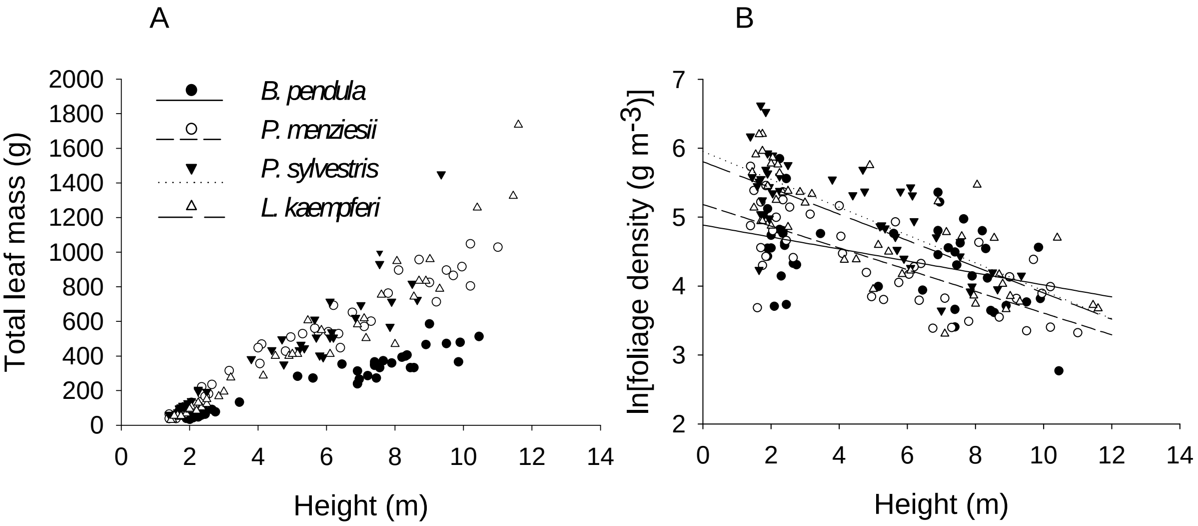

Figure 5-4. A: total leaf mass (g), and B: log-transformed foliage density (g m^{-3}) in relation to tree height

Crown volume

Crown volume depended on DBH (dataset 4, ANOVA, p<0.0001) and showed a large overlap among species, especially in the 5-yr community. There nevertheless were average species differences in the 15-yr community (p<0.01) but following a different ranking compared to RCD. Least squares estimates (at average DBH and for the 15-yr community) for crown volume in ascending order are 8.0 and 8.8 m^3 for *P. sylvestris* and *B. pendula*, and 11.7 and 12.6 m^3 for *L. kaempferi* and *P. menziesii* respectively. Species differences were less clear however. *B. pendula* (p<0.05) and *P. sylvestris* (p<0.01) significantly differed from *P. menziesii*, and *P. sylvestris* differed from *L. kaempferi* (p<0.05). Other contrasts were not significant.

Foliage mass and foliage mass density

Total foliage mass increased with tree size, but this differed between species (Fig. 5-4A). We used height as a measure for tree size because DBH was already used in the allometric function to estimate foliage mass. *B. pendula* had an overall lower leaf mass whereas the other species were undifferentiated. As the total leaf mass data are the result of regression estimates no further analysis on between-species differences was done. The log-transformed foliage densities showed a declining relationship with height (Fig. 5-4B). These data are based on independent measurements on crown volume and allow further analysis. The slope of the relationship is the same for *P. menziesii*, *P. sylvestris* and *L. kaempferi*, and only *B. pendula* is different (dataset 4, ANOVA, p<0.01). The intercepts are also different between species (p<0.0001), *P. sylvestris* and *L. kaempferi* form a group with the highest seedling foliage densities and do not differ from each other ($p=0.467$). The group with the lowest seedling foliage densities was formed by *B. pendula* and *P. menziesii*, which also did not differ ($p=0.182$).

Competitive effects

Target and neighbor species, ontogeny and competitive status all had a significant effect on the relative crown depth (RCD) of a target tree (dataset 4, ANOVA, overall model $p<0.0001$, $R^2=0.68$, see Table 5-1). This result is based on all 179 tree-pairs from both communities, with trees ranging in size from 1.35 to 12.05 m height.

There was an overall effect of neighbor tree species ($p<0.05$) even when accounting for size differences ($CSA_{0.66}$). Despite this overall result, none of the species-specific neighbor effects were significant at the 0.05 level. The overall neighbor effect was nevertheless mainly caused by *P. menziesii* as it had a threefold stronger and negative effect on RCD compared to the other three species. This effect was however not strong enough to be statistically significant.

Crown size and position ($CSA_{0.66}$) had a clear effect ($p<0.0001$), but the effect was not so much caused by the neighbor species ($p=0.599$), but rather by the target species ($p<0.01$). An ontogenetic effect was again clear as RCD was influenced by DBH ($p<0.0001$).

Strikingly, the variable target species explained most of the variation in the dataset as its sum of squares was 7 to 19 times higher than the other significant variables. The second highest explanatory value came from the competition index, the one significant interaction term shows that this was again mainly related to the target species.

Table 5-1. Analysis of variance showing the contributions of target and neighbor species on relative crown depth (RCD)

Source	DF	Type III SS	Pr > F
Target species	3	2.089	<.0001
Neighbor species	3	0.108	0.0465
DBH (target)	1	0.223	<.0001
$CSA_{0.66}$ (neighbor)	1	0.301	<.0001
$CSA_{0.66}$ * n-species	3	0.025	0.5992
$CSA_{0.66}$ * t-species	3	0.206	0.0019

When replacing the qualitative variable neighbor species by total foliage mass (in dry weight, g) or foliage mass density (g m^{-3}), the problem arises that these variables are significantly correlated with the competition index $CSA_{0.66}$ (dataset 4, Pearson's r 0.68 and −0.43 respectively, $p<0.0001$). The more foliage mass, the larger the crown and therefore crown surface area—and hence $CSA_{0.66}$—will be. Crown volume in turn, used in calculating foliage density, is directly related to crown surface area. As a result of this collinearity $CSA_{0.66}$ is henceforth dropped from the analysis.

The total foliage mass of a neighbor tree had a significant effect on the RCD of a target tree (dataset 4, ANOVA, $p<0.0001$, overall model $p<0.0001$, $R^2=0.69$, see Table 5-2). We additionally found a strong interaction between the total foliage mass of the neighbor tree and the DBH of a target tree ($p<0.0001$). Foliage mass density also had an influence on RCD (dataset 4, ANOVA, $p<0.05$, overall model $p<0.0001$, $R^2=0.61$, see Table 5-2), but the sums of squares indicate that it has a lower explanatory power than does total foliage mass (0.068 versus 0.572). There was no interaction with the DBH of a target tree ($p=0.886$) so it was left out of the final analysis as presented for foliage mass density in Table 5-2. Overall, total foliage mass contributed much more than foliage mass density in explaining the RCD of target trees, but, importantly, both factors contributed little compared to the effect of the target tree species itself.

Table 5-2. Two analyses of variance showing the contributions of target species and the total foliage mass (TFM) or foliage mass density (FMD) of a neighbor tree on relative crown depth (RCD)

Source	DF	TFM Type III SS	Pr > F	FMD Type III SS	Pr > F
Target species	3	3.112	<.0001	3.753	<.0001
TFM (neighbor)	1	0.572	<.0001	*n.a.*	*n.a.*
FMD (neighbor)	1	*n.a.*	*n.a.*	0.068	0.037
DBH (target)	1	0.267	<.0001	0.264	<.0001
TFM(n) * DBH(t)	1	0.321	<.0001	*n.a.*	*n.a.*

Discussion

Do species vertically stratify according to light demand and/or foliage mass density?

The average CPIs indicate that species stratify already in the sapling stage, as *B. pendula* and *L. keampferi* overtop *P. menziesii* and *P. sylvestris*. Genetic differences, competition and mortality had not yet created a diverse stand structure at the very early age of 5 years, but at 15 years a vertical stratification was already clear. This appears to be related to the differences in slenderness between species (see Fig. 5-2).

When comparing the current local data with data from a larger area, then this appears to be a consistent phenomenon in dense young stands of these species despite environmental variation (Dekker et al., 2007). Slenderness is an inherent morphological property, and in our study was independent of crown illumination. This is supported by other studies that found that phenotypic plasticity of tree and crown architecture is limited relative to genetic predisposition, leading to species-specific morphologies (Sterck and

Bongers, 2001; Kohyama et al., 2003; Poorter et al., 2003; Osada et al., 2004). The lack of an effect of age on tree heights indicates that the observed stratification is not the result of different establishment times between species. The vast majority of individuals in our data have established over a 5 year period after gap formation, without differences between species.
This stratification is however not strictly related to light demand. This is most strongly indicated by *P. sylvestris* which is a highly light-demanding pioneer (Burschel and Huss, 1997; CABI, 2005) but is a species of low stature and therefore on average attains the lowest crown position of all species. *B. pendula* and *P. menziesii* however do separate according to their respective light demanding and shade tolerant classification in the Netherlands. *Larix kaempferi* is more intermediate between these extremes. This is shown by its large proportion of tall and dominant individuals, in addition to the lack of clearly suppressed trees among the overtopped individuals.

Foliage densities do not diverge much between species. There is, however, a clear decline in foliage density with increasing tree size. As a tree crown increases in size, light levels deep within the crown become too low and foliage is subsequently found in a shell around the periphery (Oliver and Larson, 1996), thus decreasing whole-crown foliage density.
The three gymnosperm species show a very similar ontogeny of foliage density, but the angiosperm *B. pendula* differs. Its different ontogeny might stem from an environmental filter (only successful individuals with high foliage mass or foliage density are left in the bigger size classes), or a phylogenetic effect (only *B. pendula* is a flexible angiosperm species and those individuals that reach an emergent position might increase allocation to foliage). There is however too much variation and overlap in the data to draw conclusions on species-specific differences in the ontogeny of foliage density.
The species ranking in foliage densities is not related to differences in shade tolerance as the strongly light-demanding *P. sylvestris* (Mayer, 1992; Burschel and Huss, 1997) shows a higher foliage density than does the shade-tolerant *P. menziesii* and the more intermediate *L. kaempferi*. Similarly, at bigger sizes the pioneer *B. pendula* has the highest foliage density of all species. We therefore conclude that the results do not support our first hypothesis: species do not stratify according to light demand or foliage density. Furthermore, foliage density is not strictly related to light demand but is confounded by ontogeny and phylogeny.

Do species with a higher foliage mass density exert a stronger competitive pressure?

The species of a neighbor tree significantly affects the RCD of a target tree. However, the level of the response is far more determined by the target tree species itself. This does not change when the qualitative variable indicating the neighbor tree species is replaced by a quantitative estimate of its total foliage mass or foliage mass density. By selecting tree pairs of all possible relative sizes, these results are independent of the actual occurrence of vertical stratification between species. We therefore interpret our results as showing that at this stage in stand development, target tree identity is more important than competitor identity. Or in other words, in (juvenile) neighborhood competition the response of a target individual is stronger than the effect of its neighbor, while additionally these neighbors are functionally equivalent (cf. Uriarte et al., 2004). This is confirmed by the interaction term with the competition index, which is significant and far stronger for the target tree as compared to the neighbor tree (Table 5-1). As pointed out by Goldberg and Barton (1992) a significant interaction term between the target tree and a measure of the abundance of a competitor tree (in our case the competition index in which abundance is given by crown size) is the correct indicator for a competitive *response*.

Functional equivalence of competing species has been much studied. Next to a clear effect of overall crowding, all possible neighbor effects ranging from negative, null, and positive have been found (Hubbell et al., 2001; Peters, 2003; Uriarte et al., 2004; Zhao et al., 2006). However, these studies incorporated the full neighborhood of an individual target tree, thereby incorporating all density-dependent effects like host-specific herbivores and pathogens, root competition etc. We only aimed to investigate the effect of one tree on the RCD of another, and our data therefore only contain information on the interaction in light capture between two sapling trees. To our knowledge this is not done before, but our results suggest that it is effective. We showed that, despite indications that the shade-tolerant *P. menziesii* exerts the strongest competitive effect, the effect of having a particular neighbor is small compared to the target species’ sensitivity to light depravation. This effectively suggests a functional equivalence of the competing neighbors at this stage.

It should be noted however that species’ responses to light can change during ontogeny (Lusk, 2004; Lusk and Piper, 2007), and responses may therefore be different at a later stage. In addition, competitive interactions may also not yet be that strong because height differentiation is still ongoing. Interactions will likely become stronger once these species can fully overtop one another, and light would have to travel longer distances through the canopy to reach overgrown trees. Canham et al. (1994) and Canham et al. (2004) found a profound effect of crown characteristics on forest succession under such circumstances.

The total foliage mass of a neighbor tree has a stronger effect on the RCD of a target tree than does foliage mass density. The positive correlation between the total foliage mass of a neighbor tree and the DBH of a target tree is caused by the strong increase in tree size between the two communities. If a tree is larger, then the surrounding trees will also be larger, and as a tree is larger it is also likely to have more foliage mass. After correcting for this interaction, which is not of interest in itself, the target species and its DBH show an approximately equal effect in both analyses, whereas the contribution of total foliage mass is far stronger than that of foliage mass density.

Foliage mass is reportedly not as closely related to total light capture—and thus attenuation—as leaf surface (Yokozawa et al., 1996; Bartelink, 1998). However, leaf clustering (Bartelink, 1998) and leaf angle (Falster and Westoby, 2003) play an important role as well in radiation interception. So even though the data could be converted to a total leaf area (or leaf area density) using local values for the specific leaf area (SLA) of each species, without information on leaf clustering, leaf angles as well as within-crown variation in SLA, this would not give a better picture of the true light capture. We have therefore not attempted to do so.

The contribution of total foliage mass is relatively low as compared to the effect of target tree species in the analysis. Foliage mass density has even less influence on RCD which shows that light extinction is more determined by absolute crown depth and not by differences in light extinction per unit depth of crown (Canham et al., 1994; Bartelink, 1998). This is illustrated by the fact that *P. menziesii* has the strongest effect on a target species while having a low foliage mass density, but simultaneously having the deepest crowns of all species. Therefore, even though the shade-tolerant *P. menziesii* as a neighbor tree does appear to exert the strongest competitive pressure, we conclude that our second hypothesis is not supported: a stronger competitive effect of a species is not related to having a higher foliage density per unit crown volume. Moreover, competitive effects are more strongly related to the target species' identity than to the competitor species' identity.

Implications for stand development

Forests in the Netherlands often consist of a mosaic of monospecific and mixed-species stands of both indigenous and non-indigenous species. Under current forest management guidelines (LNV, 2000; MCPFE, 2000), these species now naturally regenerate and form communities of species growing outside of their indigenous range and outside their realized niche as seen in paleoecological records or native old-growth forests (Mayer, 1992; Richardson and Rundel, 1998; Franklin et al., 2002). Traditional species classifications such as 'light-demanding pioneer' or 'shade-tolerant climax species' may therefore not be fully applicable anymore as species have been classified in other conditions than under which they now occur, e.g. the gap assemblies in this research. *P. menziesii* for example is known as an intermediately light-demanding species in its native range (Burns and Honkala, 1990), but is considered a highly shade-tolerant species in the Netherlands. Furthermore, the autogenic development of these species assemblies in an unmanaged plant community (i.e. succession) falls outside of present day experience, despite the fact that individual species are well known in traditional silviculture (Burschel and Huss, 1997). In this final section we will therefore explore the possible implications of our results for stand development, though necessarily on a hypothetical basis.

The differences between species in their height per unit DBH (slenderness, see Fig. 5-2) are similar to our previous results (Dekker et al., 2007). Despite the overall variation in slenderness there is less variation within species than between species, revealing the relatively fixed ontogenetic trajectories of these species under the studied conditions. This likely resulted in the observed stratification as the species ranking in slenderness displays the same two groups as do the average CPIs. Furthermore, the data of Dekker et al. (2007) suggest that *P. menziesii* and *P. sylvestris* have a slightly higher diameter growth rate—even though this is not significant—so the fact that these two species are overtopped cannot be explained by having a lower growth rate. The consistent differences between species in their realized heights, i.e. a stratification in which *B. pendula* and *L. kaempferi* overtop *P. menziesii* and *P. sylvestris*, appear to be driven by consistent differences in slenderness. This illustrates an important point: a species' morphology (partly) lies at the basis of its competitive position and therefore influences subsequent stand development.

As a result, the extremely light demanding *B. pendula* as well as the intermediate *L. kaempferi* occur under high light conditions, whereas the vast majority of the also extremely light demanding *P. sylvestris* occurs under moderate to low light conditions, just like the shade tolerant *P. menziesii*. This has implications for tree vigor. A large part of the *B. pendula* and *L. kaempferi* individuals are full-crowned dominant or co-dominant trees, while *P. menziesii* is not much affected by its subordinate position with only few suppressed individuals. *P. sylvestris*, however, has a large share of suppressed trees in its population. This indicates that the traditional classification no longer applies to all species in this community: being of low stature but of high light-demand like *P. sylvestris* would be anomalous in a light-competitive community, but in our case reflects the different ecological niche of a species that evolved in primary succession environments (Richardson and Rundel, 1998). It also provides a hint of its likely future. As *P. sylvestris* can hardly maintain a canopy position in competition with the other species, it will not be able to capture enough light for long-term survival. Thus, importantly, a species' morphology is linked to its potential competitive exclusion. Therefore, if local management objectives require this species to be maintained, it will require liberation from competition. Alternatively, this species might locally survive in clumps of conspecifics.

CHAPTER 6

Effects of canopy position on radial growth, height growth and mortality of saplings in mixed dense young stands

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Submitted

Introduction

Forest gap regeneration is rarely homogenous, and saplings competing within a gap can differ considerably in size. Size differences between individuals result from differences in time of establishment, neighbourhood density, and microsite conditions (Huston, 1994; Oliver and Larson, 1996). Additionally, size differences between species result from genotypic differences in growth rate and slenderness (King, 1994; Westoby, 1998; Poorter et al., 2003).
Interspecific differences in height are particularly important as taller individuals are able to gain a disproportional part of the incident light (Franco and Kelly, 1998; Schwinning and Weiner, 1998) which can have a critical effect on growth and survival depending on a species' light demand (Kohyama, 1993; Grime, 2001; Sterck et al., 2003). Therefore, both a species' growth rate as well as its shade-tolerance (or better: persistence) are important factors in the interspecific competition for light. Stable coexistence has been proposed to occur along a trade-off between high-light growth and low-light survival (Kobe et al., 1995; Reich et al., 2003; Kitajima and Poorter, in press). This growth-survival trade-off stems from a trade-off in carbon allocation to either growth on the one hand, or storage and defense on the other hand (Poorter and Kitajima, 2007), and is found in both tropical (Kitajima, 1994) and temperate tree species (Walters and Reich, 1996).

Previous research in dense and highly competitive sapling communities in temperate forests of the Netherlands has shown that, based on differences in effective height growth (i.e. height per unit aboveground biomass), species already vertically stratify in the gap building phase (Dekker et al., 2007). Even though individuals were plastic in their response to the environment, the morphological variation within species was smaller than differences between species, as was also found in other studies (Sterck and Bongers, 2001; Kohyama et al., 2003; Poorter et al., 2003; Osada et al., 2004). The resulting vertical stratification led to a strong competition for light which affected species differently, i.e. lower statured trees of light-demanding (pioneer) species more often showed reduced vitality compared to shade-tolerant species (Dekker et al., 2008).
At first sight, these results appear to be in line with the growth-survival trade-off, but nevertheless it remains unclear what the effect is of light availability on growth, and subsequently the effect of low growth on mortality, under field conditions. Field conditions, contrary to controlled experimental conditions, incorporate unpredictable environmental fluctuations that occur over time, and multiple stressors such as competition, nutrient deficiencies and drought. If the component species of a dynamic plant community still consistently differ in their growth and survival in contrasting light conditions, then this would allow their

coexistence through niche partitioning, as proposed by the growth-survival trade-off.
For example, Lin et al. (2002) found a growth-survival trade-off under field conditions for saplings of seven co-occurring sub-tropical tree species. Niches overlapped, but a growth-survival trade-off did contribute to light gradient partitioning and coexistence. Seiwa (2007) reported similar results for seedling growth and survival in relation to gap size in a temperate forest. His results also suggested a light-gradient partitioning leading to species coexistence. In a tropical forest, Poorter and Arets (2003) showed niche separation for saplings of ten species of trees as a result of differences in growth and survival, allowing their coexistence in a narrow range of light environments. Often, however, the field data on which results are based span only a few years, leaving out the long-term effects of competition and environmental fluctuations on growth and survival. As long-term chronosequences are laborious and costly to collect, alternatively tree rings can be studied to analyze radial growth and survival of saplings in relation to light and under field conditions (Kobe et al., 1995 and ensuing publications).

The objective of this research is to investigate (i) whether saplings of different light demand differ in their growth response to light availability, and (ii) whether persistent low growth enhances the chance of mortality. To do so, we chose a long-term retrospective approach by means of dendrochronology. The study was conducted in dense sapling communities under high competition and under additional sources of stress (mainly drought). We focus on four species which co-occur in gaps in the Netherlands, i.e. Silver birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.), Japanese larch (*Larix kaempferi* Carr.) and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco). The two latter species are non-indigenous, and the natural development of communities of these four species beyond the gap building phase is unknown so far. The development of such mixed communities is important however given the contemporary European guidelines to promote both native species and autogenic processes in forest management (MCPFE, 2000). We will specifically address the following questions: 1) how does radial growth over time vary with light availability; 2) what are interspecific differences in growth responses depending on a species' light-demand; and 3) how do species differ in the probability of mortality depending on radial growth. We hypothesize that light-demanding species show a stronger (and negative) response to decreasing light availability and have a higher probability of mortality under reduced growth conditions than do shade-tolerant species.

Materials and methods

Species and study sites

Our four focal species differ in light demand during their juvenile phase, ranging from the extremely light-demanding Silver birch and Scots pine, to the comparatively shade-tolerant Douglas fir (Mayer, 1992; Burschel and Huss, 1997). Japanese larch is intermediate between these extremes (CABI, 2005; Dekker et al., 2007). These four species dominate the natural regeneration in gaps in Douglas fir forests in the Netherlands.

We collected our data in the densely forested Veluwe area, centrally located in the Netherlands. We always harvested saplings in dense fully-stocked gaps of similar species composition and left undisturbed by management. Our research area was the southern part of the Hoge Veluwe National Park (52°2'14"N, 5°50'41"E) where we selected a total of five sample sites. All sites had humic podzol soils in coarse sand with low water-holding capacity and nutrient content (Anonymous, 1975). Long-term annual temperature at the nearest weather station is 9.4° C, the warmest month is July with 17.2° C on average, the coldest is February with –0.6° C. Average annual precipitation amounts to 860 mm, more or less equally distributed over the year (KNMI, 2005).

Data collection

We used tree-ring analysis to study responses of saplings and trees to environmental conditions (cf. Pollmann, 2003; Rozas, 2003), and to assess mortality as a function of previous growth (cf. Bigler and Bugmann, 2004; Bigler et al., 2004). As diameter growth is strongly related to height growth and biomass increment in the four studied species (Dekker et al., 2007; Dekker et al., 2008) it can be taken as an indicator of whole tree growth.

Saplings were harvested in the spring and summer of 2005. The live saplings were randomly collected from different canopy positions, used as a proxy for light availability. For this we used a five point Canopy Position Index (CPI) ranging from 1) the tree does not receive direct light, to 2) the tree receives direct lateral light, 3) the tree receives direct overhead light on part of the crown, 4) the tree receives full overhead light on the whole crown, and 5) the tree has an emergent crown that receives light from all directions (Clark and Clark, 1992). This ordinal-scale visual estimation is used in both tropical and temperate forests (Jennings et al., 1999) and provides sufficient accuracy to differentiate between the ecological strategies of species (Poorter et al., 2005; Sheil et al., 2006). We harvested six live individuals per species per CPI class, yielding a total of 120 live saplings.

The dead saplings were collected together with the live ones. We selected individuals that were fully overtopped, did not have an obvious alternative cause of death (e.g. damage) and therefore most likely died from light starvation, and showed signs of being recently dead. 'Recently dead' was evaluated by checking whether a tree still had the remains of a crown (i.e. fine branches, not leaves), had to some extent flexible twigs, did not have an advanced level of stem rot at ground level, and did not have its stem and branches covered with algae, mosses or fungi. Together, such characteristics are reasonably accurate in discerning between 'recently dead' and 'long dead' trees (Kobe et al., 1995; Kobe and Coates, 1997). In the case of deciduous trees (Silver birch and Japanese larch) an individual was considered potentially alive, and was thus rejected, when it still had non-blackened buds and/or if the fine twigs were very flexible and moist inside. Based on the ages of the live and dead individuals (see Table 6-1, Results section) we estimated that recently dead in most cases is not more than five years dead. As we deliberately investigated saplings under field conditions, both the exact time and cause of death will to some level remain unpredictable. Unpredictability and variability are fundamental elements of ecosystems however, and we therefore look for an ecologically relevant signal (growth and survival differences between species) beyond this environmental noise (compare the 'ecological development' concept of Soltis, 2005).

After recording CPI, height (m), and dbh (cm) we cut down the tree and took a stem disc at ground level. These discs were air dried and sanded (up to 800 grit) to obtain a smooth surface so that tree-ring boundaries were clearly detectable. Tree-ring width was measured with a precision of 1/100 mm along two perpendicular radii using a LinTab measuring stage from RinnTec. The two tree-ring series per tree were subsequently averaged. A number of stem discs from the dead individuals showed an advanced level of decay making it impossible to accurately measure the tree rings. These samples were discarded, after which we were left with a total of 158 dead saplings. Finally, we made an empirical estimation of mortality by counting dead and live individuals of the four species along three transects (NW-SE, NE-SW, E-W) in the large 15-yr old gap. In total we counted 534 individuals which we used to calculate species-specific fractions of dead individuals. This is an estimate of the 5-yr mortality rate since we applied the same criteria as described above to identify recently dead trees.

Data analysis

Radial growth

We used the tree-ring series to construct a mean chronology per species for both live and dead individuals. This was done by averaging the tree-ring widths for each year (Orwig and Abrams, 1995; Pollmann, 2003; Rozas, 2003; Bigler and Bugmann, 2004). To document the variation in radial growth through time these mean curves were plotted together with the raw tree-ring series. For the live saplings of each species we created a mean curve per crown position at harvest (CPI). Interpretation of the annual variation through time was beyond the scope of this study as ring widths in self-thinning saplings are mostly determined by light competition, and any climate signal will be too weak for accurate cross-dating (Wyckoff and Clark, 2002). This holds especially true for short tree-ring series as in our case. Instead, we focussed on the growth level and the growth trend, separated in initial growth and final growth, i.e. the last formed five rings before death or harvest. We finally calculated average diameter and height-growth rate by dividing the dbh and tree height at harvest by the age of the tree. Differences between species were subsequently tested with a non-parametric Kruskal-Wallis test.

Initial growth, final growth and crown position

As a crown position only applies to the moment of harvest and does not necessarily apply to the whole life span of a sapling, we checked whether a dominant or suppressed tree at the time of harvest always displayed a high or a low growth level. To do this, we ranked our data and selected for each species the 12 trees that displayed the highest growth in the first three years after establishment, as well as the 12 trees that displayed the lowest growth directly after establishment, so 24 out of the 30 live trees per species (80%) were part of the analysis. This avoids generating results based only on 'extreme' trees. A period of three years averages out random single-year fluctuations but is short enough to indicate a fast or slow start for a seedling. For each of the four species we tested whether initial and final growth, as well as CPI, differed between the two groups using a Kruskal-Wallis test. We additionally correlated initial growth with both final growth and crown position at harvest by calculating Pearson's *r*. A positive relationship would indicate a trend in which trees that have a fast start continue to profit from this head start and end up high in the canopy, thereby linking CPI at harvest to a tree's growth history.

Average 5-yr final growth

For each individual we calculated the average radial growth of the last five years prior to death or harvest. We used this for the analysis of growth under different light availability, as well as for the analysis of mortality. The choice for this 5-yr period was made after doing a Wilcoxon rank sum test for a difference in average growth between live and dead individuals, using the growth over the last 5 yrs, 4 yrs, and 3 yrs respectively. The analysis with a 5-yr period had the highest significance, and therefore yields the clearest differences in growth between live and dead individuals. Results using the 3, 4 and 5 yr periods were very similar however, so the choice of period is not critical. This was also noted by Wyckoff and Clark (2002) and Kobe et al. (1995) who similarly used a 5-yr average growth period. We performed a Kruskal-Wallis test to analyze differences in radial growth within species, depending on CPI.

Modelling and estimation of mortality

To analyse the relationship between radial growth and mortality we applied the model of Kobe et al. (1995) and Kobe and Coates (1997). It is based on a Maximum Likelihood method that estimates species-specific parameters of functions that model a sapling's probability of mortality based on recent growth. Mortality probability in our case covers a period of 5 years, our limit of 'recently dead'.

Let *m*(g) represent the probability of mortality at a given growth rate *g*, and *h*(g) the probability density of all growth rates. The expectation of mortality $\overline{U}$ is then given by:

$$\overline{U} = \int_0^\infty m(g)h(g)dg$$

Let *D* denote the number of dead saplings which were found in a transect of *N* individuals, *Q* the number of dead stems, indexed by *i*, for which the growth rate is available, and *R* the number of live stems, indexed by *j*. Kobe et al. (1995) show that the likelihood *L* for such a dataset is given by:

$$L = (\overline{U}^{D})(1-\overline{U})^{N-D} \cdot \prod_{i=1}^{Q} \frac{m(g_i)h(g_i)}{\overline{U}} \cdot \prod_{j=1}^{R} \frac{\{1-m(g_j)\}h(g_j)}{1-\overline{U}}$$

Maximum likelihood can be employed to estimate parameters of the functions *m*(g) and *h*(g). We used a gamma density with parameters *α* and *β* to specify *h*(g):

$$h(g) = \frac{g^{\alpha-1}\, \beta^{\alpha}\, e^{-g/\beta}}{\Gamma(\alpha)}$$

For the probability of mortality *m*(g) we used an exponential decay with parameter *A* and *B*:

$$m(g) = Ae^{-Bg} \quad \text{where } 0<A\leq 1 \text{ and } B>0$$

These are the same functional forms as used by Kobe et al. (1995), only the gamma density is parameterized differently. The expectation of mortality can then be written in closed form:

$$\overline{U} = A(B\beta+1)^{-\alpha}$$

In fitting these equations per species the likelihood *L* is maximized of obtaining the current dataset as a function of *i*) the probability of encountering *Q* dead saplings and *R* live saplings, *ii*) the product of the probability densities that a dead sapling had growth history g_i prior to death, and *iii*) the product of the probability densities that a live sapling had growth history g_j.

Our main interest was in the parameters *A* and *B* of the exponential mortality function which contain information on differences in growth-related mortality between species. We tested whether A=1, i.e. whether zero growth implies certain death. Note that *A*=1 is on the boundary of parameter space and an ordinary likelihood ratio test is not available. We therefore used a nonparametric bootstrap test which employs the observed data to approximate the unknown sampling distribution of a test statistic by sampling observations with replacement (Efron and Tibshirani, 1994). The test statistic used was the difference in log-likelihood for the model with *A*=1 and the model with 0<*A*≤1, and we used 1000 bootstrap samples. A single bootstrap sample consisted of three parts, all drawn with replacement: a sample of size *Q* from the dead trees, a sample of size *R* from the live trees, and a sample of size *N* from the transect data. The nonparametric bootstrap, with 1000 bootstrap samples, was also employed to create 95% confidence intervals for the parameter estimates, and thus for the mortality curves.

Results

Radial growth of live and dead saplings

All live saplings experienced a growth decline over time after an initial period of high growth. On top of this age-related growth trend, the relative positions of the mean curves per CPI show a growth reduction when trees have a less favourable crown position, with the exception of Douglas fir (Fig. 6-1). Overall, growth levels across species were broadly in the same range. Fully overtopped individuals of the shade-tolerant Douglas fir, however, on average never reached the low growth levels (<1 mm y^{-1}) of comparable individuals of the other species.

Table 6-1 presents the average dbh, height and age for both live and dead individuals per species. For the live saplings we checked for differences in height and diameter growth, across CPIs. Diameter growth rates (in cm y^{-1} ± s.d.) for Silver birch, Douglas fir, Scots pine and Japanese larch were 0.36 (± 0.14), 0.34 (± 0.10), 0.35 (± 0.11), and 0.33 (± 0.13) respectively, and were not significantly different (p=0.823). Average height growth rates (in m y^{-1} ± s.d.) significantly differed between species (p<0.0001) and were 0.61 (± 0.16), 0.36 (± 0.09), 0.37 (± 0.06), and 0.42 (±0.11) respectively. Dead individuals on average grew significantly slower prior to death (p<0.05) than did the harvested live individuals in all species except Japanese larch (p=0.648).

In Douglas fir, the differentiation between individuals with respect to their final crown position (CPI) occurred in approximately the first six years of their life (Fig. 6-1). After that, growth between trees of different CPI (measured at harvest) did not differ systematically. The differentiation according to CPI in Silver birch and Scots pine was more consistent over the whole life span, with the exception of the initial years after establishment. In Japanese larch, growth with respect to current CPI was separated into two groups. Individuals that received high light (CPI 4 and 5) by far outgrew individuals that received average to low light (CPI 1 to 3).

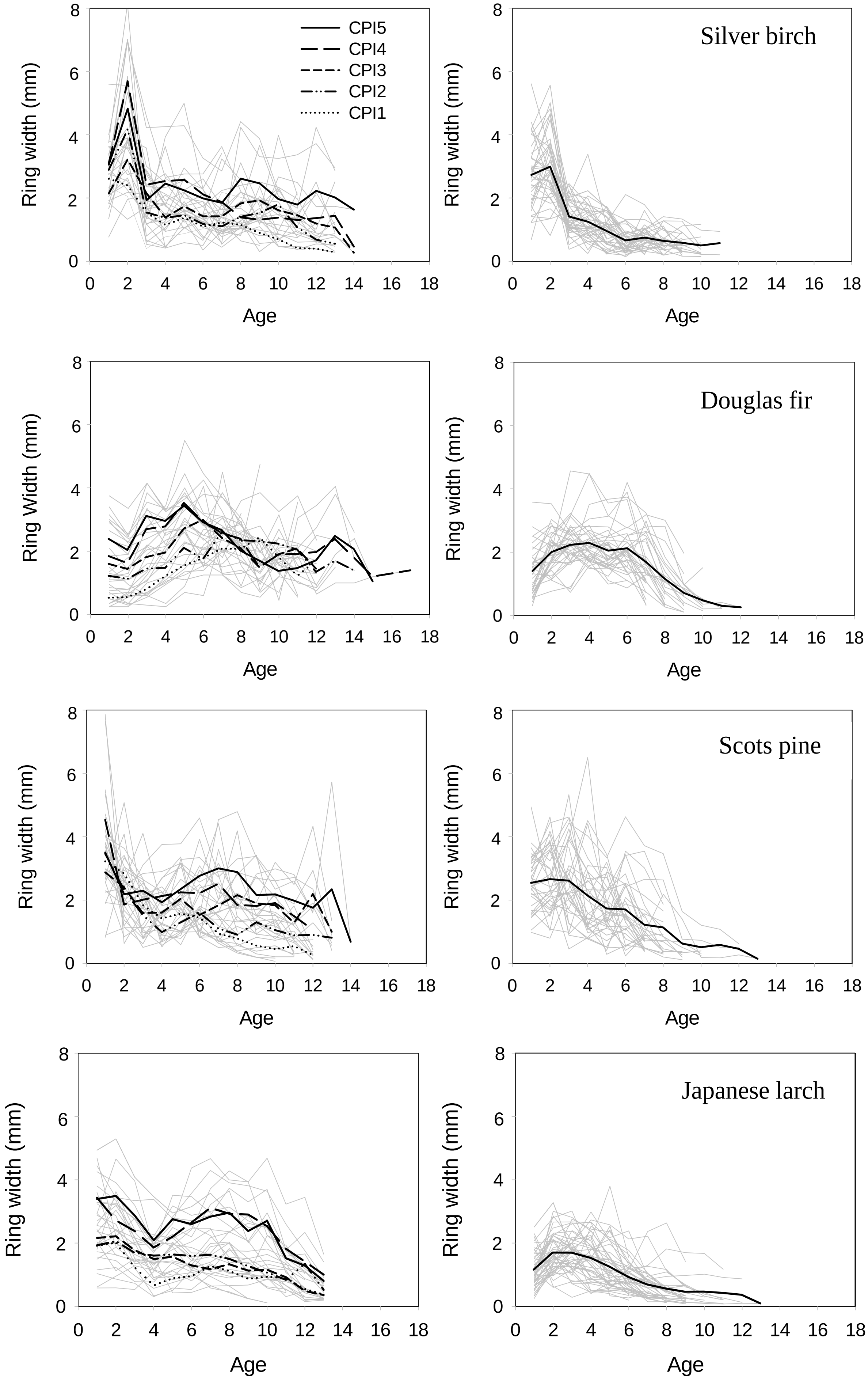
The mean radial growth curves of fully overtopped (CPI = 1) individuals of Silver birch, Scots pine and Japanese larch showed a similar growth pattern as those of the dead, light-starved individuals (Fig. 6-1). In Douglas fir, however, fully overtopped individuals had a constant growth rate whereas individuals that died showed a gradual decline in growth rate starting approximately eight years prior to their death. Dead trees of Silver birch, Scots pine and Japanese larch all showed a strong growth decline over time. Scots pine however displayed a highly erratic growth prior to death, whereas the long and flat tail in Japanese larch suggests that this species can persist at low growth for some time. Overall, growth reduction was a gradual and long-term process in all species but mortality occurred when radial growth was consistently reduced to approximately half a millimetre per year.

The data furthermore show that variation in past growth can be large in both live and dead individuals of all species (Fig. 6-1). Important to note is that at higher ages fewer trees remain to make up the mean curves, which therefore can display sudden fluctuations towards the end of the series.

Correlations between initial and final growth and crown position

The two groups of low and high initial growth differed significantly, as indeed we set out to do, showing that newly established individuals can have a wide range in growth (Fig. 6-1, Table 6-2). In Silver birch and Japanese larch, high initial growth correlated with high growth later in life. This correlation however was rather weak and did not lead to a significant difference in radial growth between the two groups prior to harvest. This suggests that the initial differences in radial growth level off over time.

For all species except Scots pine there was a significant correlation between initial growth and CPI at harvest, indicating that trees with a high initial growth end up high in the canopy (high CPI) and *vice versa.* There was no difference in the average age per CPI class for all species except Japanese larch, which had more young trees in CPI 2 (average age 11.8 years, in the other classes this ranges from 13.5 to 13.8 years) causing a significant overall difference ($p=0.021$). When comparing the groups of high and low initial growth, CPI at harvest was significantly different for Douglas fir and Japanese larch (Table 6-2). In Scots pine, initial growth is similar for all trees, and differentiation in growth as related to CPI only starts after approximately 4 years of age.



CPI5
CPI4
CPI3
CPI2
CPI1
Silver birch
Douglas fir
Scots pine
Japanese larch
Ring width (mm)
Ring Width (mm)
Age
0
2
4
6
8
10
12
14
16
18

Fig 6-1 (previous page). Individual growth curves (grey lines) and middles curves (black lines). For the live saplings (left column) a middle curve is given for all individuals of a given crown position (CPI), for the dead individuals (right column) a single overall middle curve is drawn. Note that at higher ages fewer trees remain to make up the middle curves, which therefore display sudden fluctuations towards the end of the growth series.

Table 6-1. Sample sizes and averages per species for dbh, height and age. Between brackets the standard deviation is given

Species	n		DBH (cm)		Height (m)		Age (y)	
	Dead	Alive	Dead	Alive	Dead	Alive	Dead	Alive
Silver birch	40	30	2.3 (0.4)	4.2 (1.4)	4.5 (1.3)	7.0 (1.2)	8.6 (1.4)	11.8 (1.8)
Douglas fir	36	30	2.7 (0.7)	3.9 (1.2)	3.7 (0.8)	4.0 (0.9)	8.4 (1.6)	11.5 (2.1)
Scots pine	35	30	2.9 (0.8)	4.0 (1.3)	3.9 (0.9)	4.2 (0.8)	8.1 (1.7)	11.5 (1.5)
Japanese larch	47	30	2.0 (0.7)	4.5 (1.8)	3.8 (1.2)	5.6 (1.6)	8.8 (1.8)	13.3 (1.1)

Average radial growth over the last 5 years

Average radial growth over the last 5 years, used as input in the mortality model, was reduced in the lower canopy positions (CPI 1&2) for most species except Douglas fir (Fig. 6-2). The effect of canopy position was significant for Scots pine (p=0.001) and Japanese larch (p=0.002), but not for Douglas fir (p=0.977). For Silver birch, the data show a declining trend in final growth with lower CPI, but this was not significant (p=0.144) due to the great variability in the dominant canopy positions (CPI 4-5, see Fig. 6-2).

Average growth prior to death spanned a large range (Fig. 6-2). For Douglas fir and Scots pine this even encompassed the full range in growth of live individuals. In testing for a difference between dead and live trees (including all CPIs) we found that live individuals of Silver birch (p<0.0001), Japanese larch (p=0.005) and Douglas fir (p=0.011) had experienced significantly higher growth than dead individuals, but this was not the case in Scots pine (p=0.650).

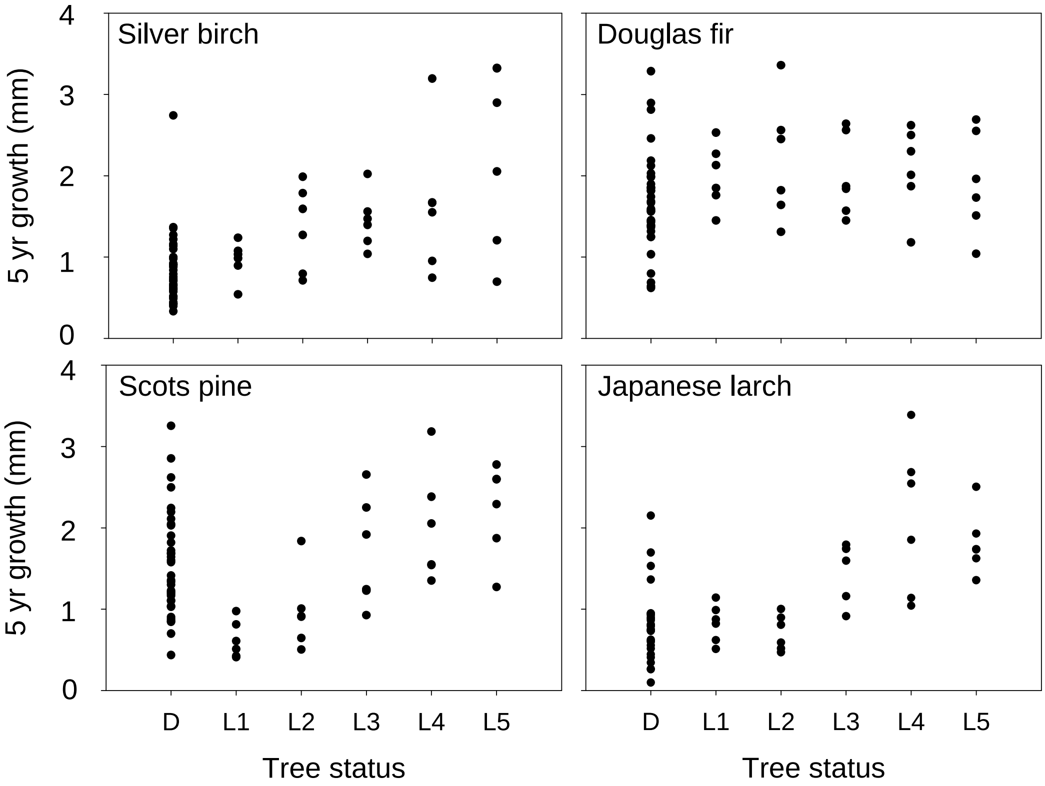


Fig. 6-2. Final radial growth (5 yr average) of trees of different status at time of harvest. L1-5 displays final growth of live individuals from different canopy positions, with the index number indicating CPI at harvest. D displays final growth of dead trees

Mortality

The empirical 5-yr mortality estimates from the transect counts (based on the number of dead individuals relative to the total number of individuals per species) were 28% for Silver birch, 10% for Douglas fir, 38% for Scots pine, and 16% for Japanese larch. Estimated mortality functions for Silver Birch, Douglas fir and Japanese larch are very similar and reveal a more or less equally declining mortality probability with increasing growth (Fig. 6-3). The curve for Scots pine is very different with no relationship between growth and the probability of mortality. We tested whether these results for Scots pine resulted from a lack of fit between growth and mortality, as suggested by Figure 6-2. We performed an *ad hoc* logistic regression between survivorship (a binary response variable indicating whether a tree is dead or alive) and average 5-yr growth (explanatory variable) to generate significance levels. This regression yielded a significant relationship for Silver birch ($p<0.0001$), Japanese larch ($p=0.001$) and Douglas fir ($p=0.011$), but not for Scots pine ($p=0.775$). Given the lack of a relationship between recent growth and mortality, the fitted mortality function yielded a flat line.

Table 6-2. Initial and final radial growth rates (3 yr average in mm y^{-1}) and final average CPI for two groups: a high initial-growth group, and a low initial-growth group. Pearson's *r* presents the correlation between initial growth and final growth or CPI respectively, n.a. means not applicable

Species	Parameter	Low initial-growth group	High initial-growth group	p-value of the difference	Pearson's r (p-value)
Silver birch	Initial growth	2.0	3.8	<0.0001	n.a.
	Final growth	1.3	1.7	0.299	0.38 (0.038)
	CPI harvest	2.3	3.4	0.077	0.48 (0.018)
Douglas fir	Initial growth	0.67	2.7	<0.0001	n.a.
	Final growth	2.1	1.8	0.371	-0.31 (0.100)
	CPI harvest	1.9	3.8	0.002	0.75 (<0.0001)
Scots pine	Initial growth	2.0	3.2	<0.0001	n.a.
	Final growth	1.4	1.5	0.707	-0.13 (0.478)
	CPI harvest	3.2	3.4	0.595	0.07 (0.733)
Japanese larch	Initial growth	1.4	3.3	<0.0001	n.a.
	Final growth	0.7	1.1	0.074	0.40 (0.028)
	CPI harvest	2.3	3.6	0.045	0.63 (0.001)

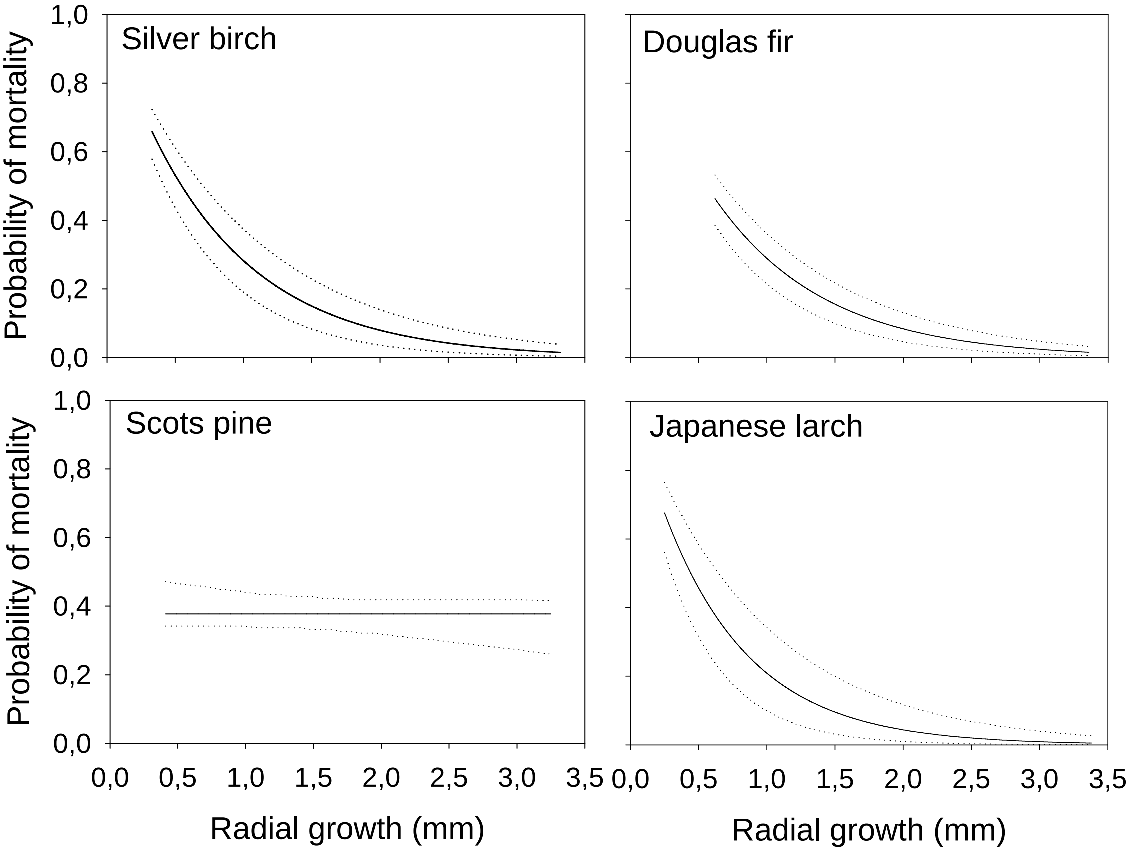


Fig. 6-3. Mortality curves with 95% confidence intervals for all species, giving the probability of mortality as a function of radial growth (5 yr average). In Scots pine the A parameter is significant (A=0.378, *s.e.* 0.035, p<0.0001), for the other species A=1. Scots pine furthermore has B=0, whereas the other species have a declining probability of mortality with increasing growth. For Silver birch B=1.256 (*s.e.* 0.156), for Douglas fir B=1.240 (*s.e.* 0.121), for Japanese larch B=1.566 (*s.e.* 0.321)

Discussion

Overall patterns in sapling growth

As plants grow bigger and crowding intensifies all species on average showed a decrease in radial growth over time, irrespective of canopy position. This is most likely caused by the increase in competition, eventually leading to self-thinning (Oliver and Larson, 1996). On top of this overall trend, light-demanding (Silver birch and Scots pine) and intermediate (Japanese larch) species responded negatively to a decrease in light availability whereas the one shade-tolerant species (Douglas fir) maintained a consistent growth level across CPIs. This difference in response was found in both the long term (tree ring series, Fig. 6-1) and the short term (average 5-yr growth, Fig. 6-2).

Initial growth in Douglas fir ultimately determined its crown position at harvest (Fig. 6-1). This cannot however be attributed to light as the seedling establishment phase is characterised by full access to light (Oliver and Larson, 1996) and overall high growth rates (Kaelke et al., 2001; Seiwa, 2007). Since the average ages did not differ across CPI classes in this species, variation in establishment time cannot explain these results either. This leaves only genetic makeup and microsite conditions to account for the observed differentiation (cf. Huston, 1994).

These results for Douglas fir do agree with the general pattern that a seedling's early growth largely determines its success later in life (Landis and Peart, 2005). Our data suggest that individuals with high initial growth after establishment have a higher chance of attaining a canopy, or even emergent position. This was however not the case for Scots pine. Radial growth determines height growth through species-specific height-diameter ratios, i.e. the height that is added to a stem for a given amount of additional diameter. These height-diameter ratios differ between the studied species, leading to differences in height growth even at a similar diameter growth (Dekker et al., 2007). Crown position (CPI) subsequently quantifies a tree's canopy height relative to the surrounding trees. In the case of Scots pine, its high radial growth was not transferred to fast height growth because of its low height-diameter ratio, which was even lower than that of Douglas fir. As it was unable to grow taller than the other species, it rarely gained a good canopy position (after which a negative feedback loop likely starts in which reduced radial growth is followed by reduced height growth, leading to an even lower canopy position). In the case of the other species, however, saplings generally continued to profit from a head start gained as a seedling, which is especially important for light-demanding species.

Interspecific differences in growth depending on light demand

Our results indicate that differences in performance between species do not occur in high light but rather in low-light conditions (Fig. 6-2). In high light all species grew at an approximately similar rate, but in low light Douglas fir outperformed the three other species. These results apparently deviate from other studies which found that under low-light conditions growth is at least equal across light-demanding and shade-tolerant species (Walters and Reich, 1996, 1999; Poorter, 2005), whereas under high-light conditions growth is much higher in light-demanding species (Poorter, 1999; Portsmuth and Niinemets, 2007). This deviation, however, is only apparent, and can be explained as follows. In this study we found that –based on whole-life performance– diameter growth rates were not, but height growth rates were significantly different between species. As Dekker et al. (2007) have shown, at equal diameter increment Silver birch and Japanese larch produce significantly more aboveground biomass than Scots pine and Douglas fir. This implies that at the common level of radial growth in high light in this study (for all species averaging around 2 mm y^{-1} at CPI 4 and 5), Silver birch and Japanese larch produced more biomass than did Douglas fir. It similarly implies that even though under low-light conditions Douglas fir outperformed the other species in terms of radial growth, this is likely reduced or even reversed when considered in terms of biomass increment. Therefore, our results corroborate the mentioned previous findings when taking a whole-plant perspective and considering biomass increment rather than radial growth.

Still, Scots pine remains the odd species out since it showed the same height growth as the shade-tolerant Douglas fir, while at the same time it showed a strong positive growth response to light similar to that of a real pioneer like Silver birch (Figs. 6-1 and 6-2). So given its reaction to both low light (reduced growth) and high light (lack of fast growth), as well as the fact that its mortality was unrelated to its growth level, Scots pine does not fit in the growth-survival trade-off. This finding warrants a word of caution for the interpretation of growth-survival trade-offs in non-natural communities, as is the case in this study. In essence, the growth-survival trade-off should lead to species coexistence by partitioning the light gradient. In communities that have been highly influenced by man through species displacements and compositional changes, secondary successional stages will include species assemblages that are greatly different from those occurring under natural conditions. Under natural conditions, ‘odd’ species like Scots pine are unlikely to be present since these will have long been outcompeted. On the other hand, viewing species within this growth-survival trade-off scheme will enable us to make predictions on the potential of newly introduced species in our ecosystems, like in our case Douglas fir and Japanese larch.

Growth and probability of mortality

We found a significant relationship between recent growth (5-yr average) and mortality for all species except Scots pine. In Scots pine the 5-yr average growth rates prior to death were too variable to establish a relationship between recent radial growth and the probability of mortality. In fact, growth prior to death spanned the entire range in growth levels of living trees (Fig. 6-2). There was no effect of sample site in this high variability as data ranges from each of the five sites fully overlapped (not shown). Competition for light is considered the main driver of mortality in young and dense self-thinning stands (Oliver and Larson, 1996). This originates from the fact that light competition is asymmetric and pre-emptive (Schwinning and Weiner, 1998; Weigelt and Jolliffe, 2003). Self-thinning in even-aged monospecific stands, for example, is driven by crown geometry and slenderness (Lonsdale and Watkinson, 1983; Weller, 1987; Ellison, 1989; Franco and Kelly, 1998), further supporting the notion that competition for light strongly determines mortality. As the main canopy rises with increasing tree height, individuals that cannot keep up in height growth but which are not sufficiently shade tolerant to survive in the understorey, will die (Oliver and Larson, 1996).

In each of our species, however, some individuals died even when displaying an (on average) relatively high radial growth rate in the 5 years prior to death. For Scots pine and Douglas fir we noted an erratic radial growth pattern with abrupt annual changes in a number of individuals, including dominant trees (Fig. 6-1). Together with the overall trend of a declining growth across species, these patterns suggest additional causes for mortality. Short-term stresses can predispose trees to die if they are already under long-term stress, and can also make trees vulnerable to otherwise relatively harmless afflictions (Pedersen, 1998a, 1998b).

In the sampled communities, light deficiency forms a long-term stress factor. Additional short-term stress in the dry sandy soils of our study area may be caused by a lack of water availability during dry years, and may have further reduced tree vigour. Pathogen infestation may be a further contributing factor to tree mortality. This particularly holds for Scots pine which is highly susceptible to Needle Cast (*Lophodermium* spp), especially when growing in dense stands (Schwerdtfeger, 1957). With a combination of predisposing, inciting and contributing stresses (Manion, 1981) tree mortality will become stochastic and irregular (Kobe, 1996; Eid and Tuhus, 2001), even in self-thinning stands. We cannot positively confirm such additional agents, but our data, which were deliberately collected under field conditions, do show that mortality in self-thinning mixed stands is not exclusively driven by light competition.

Mortality analyses for Silver birch, Douglas fir and Japanese larch did not result in significantly different mortality curves (Fig. 6-3). Average growth levels of these species under different CPIs nevertheless place them on very different parts of this apparently common mortality curve. For example, the consistent growth level of Douglas fir which was on average around 2 mm y^{-1} across CPIs, means that this species has an overall 5-yr mortality rate of approximately 10%. In dominant individuals of Silver birch (CPI 4 and 5), growing at a similar growth level of 2 mm, mortality also lies around 10%. Contrary, fully overtopped individuals of this species (CPI 1) have a mortality rate of approximately 30% as a result of their strongly reduced growth. This illustrates that in Silver birch, as well as Japanese larch, only fast-growing (radial and height growth) individuals that have secured a canopy position may survive to adulthood. Individuals of Douglas fir all have that same chance, irrespective of light availability during the sapling stage.

In Scots pine we found no relationship between mortality and growth. Results nevertheless suggest that given its strong positive relationship between radial growth and light availability, and its generally low radial and height growth, this species will experience high mortality and will likely be competitively excluded. This is supported by the high empirical mortality counts (38%, the highest of all species).

Conclusions

We conclude the following:

i) Additional short or long term stresses like pathogens or nutrient deficiency offer an important contribution to growth and mortality, showing that in dense mixed stands the competition for light is not the only factor driving self-thinning.

ii) For a growth-survival trade-off to contribute to species coexistence, high-light growth in pioneers has to mean that the carbon gained strongly contributes to height extension. In that case, niche partitioning and species coexistence are promoted through vertical stratification and light partitioning.

iii) Species in non-natural communities that do not fit in either the high growth or the high survival part of the growth-survival trade-off, like in our case Scots pine, are likely to be competitively displaced when growing and competing in natural succession. Next to explaining multiple-species coexistence in natural species assemblages, the growth-survival trade-off therefore also suggests less favourable species mixtures in man-made communities. It is however difficult to evaluate species characteristics in the light of biological trade-offs in non-natural man-made communities, due to the very different evolutionary backgrounds of species.

CHAPTER 7

Synthesis

Introduction

In West-European forestry, including the Netherlands, the last decades the main focus has shifted to close-to-nature silviculture. In practice, this means that stands are rejuvenated or transformed using natural regeneration in canopy gaps. In this thesis we focussed on gaps in Douglas fir forests, with a regeneration consisting of four species. In order to assess possible consequences of this shift in management, it is necessary to predict the community development of the species assemblages inside these canopy gaps. However, there is hardly any silvicultural experience or experimental data available that investigates such natural development, and consequently hardly any information exists on species performance and community succession in these canopy gaps. This information is, however, crucial to evaluate whether management intervention under a close-to-nature approach indeed creates the desired changes in forest composition.

To overcome the lack of data on community development and coexistence in the gap building phase, this research focused on the inherent growth patterns of the main species in the regeneration. Next to a review of the political framework outlining the societal goals for forest management, we investigated the relationship between sapling morphology (specifically stem slenderness) and its ability to compete for light, and how this determines growth and mortality. We mainly set out to test whether species stratify in height according to their slenderness and shade tolerance, thereby creating a situation of niche differentiation that promotes their coexistence. By taking basic plant traits such as height per unit biomass and emerging community traits like vertical stratification, and by connecting this to the competition for light in the self-thinning phase, I aimed to infer consequences for stand development. These consequences are the coexistence or competitive exclusion of tree species in naturally established mixed communities of native and non-native species.

In this final chapter I will scale up and evaluate the results in light of the long-term goals of close-to-nature silviculture.

The socio-political framework for forest management

In large parts of Europe, forest degradation and destruction led to open landscapes that were replanted with coniferous monocultures for wood production. As a result, of the 32 percent of the total land area of Europe now covered by forests, 87 percent is even-aged and 30 percent is monospecific. An additional 50 percent contains only 2-3 tree species (MCPFE, 2007). In the Netherlands, high forests are currently for more than 80 percent even-aged, and for more than 50 percent monospecific (LNV, 2007). These monocultures now conflict with the societal demand for forests that should deliver multiple socio-economic and nature conservation values (e.g. landscape amenity, recreational opportunities, biodiversity).

In addressing this issue, international policy documents present a homogenous picture of what is desired from forest management. The goal is to create multi-functional forests that are no longer managed for their commodity function only, and using a type of forest management that:

- maintains natural structures and processes, e.g. hollow trees and decaying wood
- uses silvicultural practices that mimic natural dynamics, e.g. natural regeneration
- refrains from intensively managed monocultures
- enhances a mixed, indigenous species composition
- works with uneven-aged stands

Similar objectives are also present in Dutch forest policy and management, where the use of natural processes (like regeneration, competition and succession) is advanced to create stable and mixed-species uneven-aged forests (Van der Jagt et al., 2000; Van den Bos, 2002).
Forest policies therefore advocate a forest management that allows natural cycles to take their course (like succession, regeneration, senescence and decay), and at the same time produces quality timber. The proposed application of close-to-nature silviculture is subsequently expected to give rise to uneven-aged and mixed-species forests, and therefore to sustainable, multifunctional, healthy and resistant forests.

Connecting (short-term) methods to (long-term) goals with close-to-nature silviculture

Two aspects specifically underlie the current attention for close-to-nature silviculture. These are that:

1. Resulting from the past establishment of plantations, forests are now often (to some degree) monospecific and artificial
2. Sustainable forest management (as adopted in forest policies and outlined in forestry science) calls for forests of high biodiversity and diverse structure, which is assumed to lead to high stability

These two aspects represent two alternative states of the forest, and close-to-nature silviculture can be applied in order to go from the first state (monospecific plantations) to the second state (mixed uneven-aged forests). This mostly involves the use of natural regeneration (cf. MCPFE, 2007).
In the Netherlands this conversion is generally done by applying Integrated Forest Management (*Geïntegreerd bosbeheer*). This approach integrates nature conservation, wood production and the output of recreational values. Integrated Forest Management is *inter alia* used to convert even-aged monocultures into uneven-aged mixed-species forests. This is done by creating gaps in stands that do not meet evaluation criteria regarding

species composition, growth level, structural variation, regeneration, dead wood, aesthetic values and presence of potential crop trees (Van der Jagt et al., 2000). By harvesting groups of trees gaps are created, which initializes the regeneration of a new cohort of trees. Consequently it creates (tree) species diversity and horizontal and vertical structure, as well as the establishment of new potential crop trees. After gap formation, the ensuing developments in the regeneration link the coarser-scale disturbances caused by forest management interventions to fine-scale processes like interspecific competition (Gratzer et al., 2004).

The gap building phase

After their establishment, seedlings experience a period of growth unhindered by competition with neighbouring seedlings. There is an influence of the surrounding mature trees though. At some point in time the individual crowns will meet (i.e. crown closure), after which the saplings will start competing for light (Oliver and Larson, 1996). During this competition saplings will expand their size at the cost of others, leading to a reduction in the number of trees per surface area: self-thinning. By intercepting more light a taller sapling increases its relative fitness directly by its enhanced photosynthesis, as well as indirectly since the resource is pre-empted and no longer available for others (Falster and Westoby, 2003). Overtopped individuals that no longer have sufficient access to light and that are not sufficiently shade tolerant, stagnate in growth and die. The high mortality during self-thinning influences species composition of the regeneration unit. A number of ecological processes are important for growth, competition and survival during self-thinning in the gap building phase. Studying these spatio-temporal processes provides a link between pattern and process in plant communities, and plays a crucial role in understanding ecosystem dynamics (Gratzer et al., 2004). Important for growth, competition and survival are:

- The species-specific relationship between an increase in size and a concomitant change in shape
- Emergent stand characteristics as a result of species' morphological differentiation
- The effect of species and stand characteristics on interspecific competition
- The effect of light availability, resulting from morphological differences and emergent stand characteristics, on growth and mortality

Sapling morphology in relation to size

The studied tree species differed when biomass and DBH were related to height. In the sapling stage Silver birch was on average taller than the other species for a given biomass or diameter, followed by Japanese larch. Shortest were Douglas fir and Scots pine. Height growth rates also differed between species but diameter growth rates did not. This disparity shows the interaction between biomass distribution and stem slenderness. Silver birch was the tallest species due to both a large stem mass fraction and a high stem slenderness. Scots pine, on the other hand, had a similarly high stem mass fraction, but a low stem slenderness. This made it one of the shortest species. Hence, biomass distribution and stem slenderness can either reinforce (in the case of Silver birch) or counteract (in the case of Scots pine) one another in terms of sapling height. Both biomass partitioning and slenderness displayed a species-specific ontogeny and our results therefore show that the inherent morphology of a sapling strongly influences its achieved height per unit biomass. In short, architecture makes a strong contribution to height.

We based the investigation of growth patterns on sampling data from several gap communities. In the analyses we calculated species-specific mass-based heights. These data deal with height on a 'per unit biomass' (or DBH) basis as a general species characteristic across communities. Differences are a consequence of species-specific biomass partitioning and slenderness. We cannot, however, based on these cross-community data, conclude that one species will actually overtop another. This requires a perspective from a single community in which co-occurring species overtop one another based on differences in establishment time and relative heights. The potential of a species to outgrow and overtop others depends on what other species (*casu quo* growth patterns) are present in a community, especially in the dense high-competition situations of gap regeneration (Falster and Westoby, 2003).

Taking such a single community perspective (Chapter 5), we showed that differences in the achieved height per unit DBH started already at an early age. This subsequently caused a vertical stratification between species that was not caused by different establishment times, and that was in agreement with the results from the sampling data (Chapter 4).

Relative crown depth (RCD) depended on sapling size and differed on average between species. Douglas fir was the only species that maintained its RCD with increasing size. A crown rise in self-thinning stands results from a decrease in light levels down the expanding canopy (Oliver and Larson, 1996; Mäkelä and Vanninen, 1998; Ilomäki et al., 2003). As Douglas fir maintained its RCD, this shows its higher shade tolerance relative to the other species.

Sapling morphology is linked to interspecific competition by the effect growth patterns will have on stand structure. As the behaviour of individuals (e.g. growth rate and mortality) can affect the composition of the community, likewise stress responses of individuals will result in community-scale effects (Pierce et al., 2005).

Light availability and morphology

It is noteworthy that despite variation in crown positions, and hence light availability, within species all individuals were positioned along relatively fixed morphological trajectories (Fig. 4-1). Silver birch showed the most variation, but it still developed along a recognizable trajectory. How can this be the case despite growth differences in individuals from exposed versus non-exposed crown positions?

In even-aged plantations, spacing (i.e. density) determines to which level individuals grow increasingly tall and thin (Zeide, 2002), so slenderness clearly is flexible. We, however, studied saplings in their natural context of dense gap assemblies. Growth under natural conditions differs strongly from spacing trials in terms of establishment, density, competition etc (cf. Soltis, 2005). Under the high-density and high-competition circumstances of gap regeneration, there is comparatively little room for the morphological variation found in spacing trials.

If the growth of individual trees depends on light availability, yet the population distribution of height-biomass values under natural conditions follows a single curve, then four non-excluding explanations can be given for this:

1. Competitive pressure allows only for high slenderness, which is genetically restrained
2. Biomass and age are correlated, so the height-biomass graph depicts height growth over time
3. Mortality probabilities for extreme phenotypes are higher in comparison to the observed phenotypes
4. Over time, due to temporal environmental heterogeneity, each individual tree will experience both good and bad growing conditions

Ad 1. Competitive pressure in a light-limited gap environment forces individuals to grow tall and thin. Species are at an advantage when they have fast height growth with sufficient diameter growth to prevent mechanical failure. Slender trees gain more height per invested unit of biomass and have a competitive advantage (better access to light at lower costs). As slender phenotypes will be favoured through higher survival, the upper limit to slenderness (determined by species-specific height-diameter ratios and wood properties) could result in the observed height-biomass curves. In other words, a tree growing under high-light conditions is simply bigger after some time, but it follows the same morphological trajectory (maximum slenderness), which is genetically restrained.

Ad 2. Height growth is primary growth, can be rhythmic and discrete, and depends strongly on age. Diameter growth is secondary growth, can continue throughout the growing season, and depends strongly on environmental conditions. The data in Fig 4-1 contain only a limited range in ages and therefore also a maximum achievable height. If the abscissa correlates strongly with age, then the observed curve simply conveys

maximum height growth over time. Variation in diameter growth (which mainly determines biomass) as a result of different growing conditions, determines the spread along the abscissa for a given height.
Ad 3. Short and thick individuals (under the main canopy) may be susceptible to increased mortality resulting from a lack of light and increased physical damage. Tall and thin individuals (above the main canopy) may suffer more from buckling, drought, cavitation and photo-inhibition. Such differential mortality probabilities would compress the population-level height-biomass curve.
Ad 4. Environmental heterogeneity will average out differences between individuals and have a dampening effect on the population-level height-biomass curve.

To illustrate, Fig. 7-1 (top figure) shows a height-biomass curve (in this case for Scots pine) with two zones delineated above and below the observed values, representing tall and thin versus short and thick individuals. Resulting from genetic limitations to phenotypic adaptation, different mortality probabilities and environmental heterogeneity, the population distribution of height-biomass values may be compressed into the observed band of phenotypes with higher survival probabilities. It is important not to confuse the distribution of height-biomass values in Fig. 7-1 with growth over time, or a chronosequence. Each observation represents an individual sapling at a single moment in time. The data present a population distribution of height-biomass values over a (limited) range of ages and communities, not a temporal development.

Static versus dynamic data
Sampling individuals in a population (static data) instead of following individuals over time (dynamic data) yields information on how a species-characteristic is distributed within a population. This distribution is the result of the past performance of the individuals in the population. In other words, the data are scaled up from the individual level (past growth and mortality) to the population level (distribution of size), thereby integrating over the effect of spatial and temporal heterogeneity, species interactions, mortality etc.
The fact, then, that crown position does not influence the height per unit biomass does not mean that individuals growing in different light regimes will not differ after any period of time. It only shows that the population distribution of height-biomass values is not influenced by the individual crown positions of saplings. Saplings of similar age but different light regime will simply take op different position on the same curve.
As such, static population level data are important in order to understand community dynamics. It allows one to evaluate the ecological limits to a plastic characteristic, in our case plant height per unit biomass. An analogy that underlines the importance of static data is given by the difference between the dynamic self-thinning line (the reduction over time in stand

density with increasing plant size in a single stand) and the self-thinning boundary line (the upper values in a static distribution of average plant size and stand density for many stands). The first gives information on how individual stands develop in time, the second presents a boundary to that development that could not be detected by looking at dynamic data alone (Weller, 1990; Pretzsch, 2001).

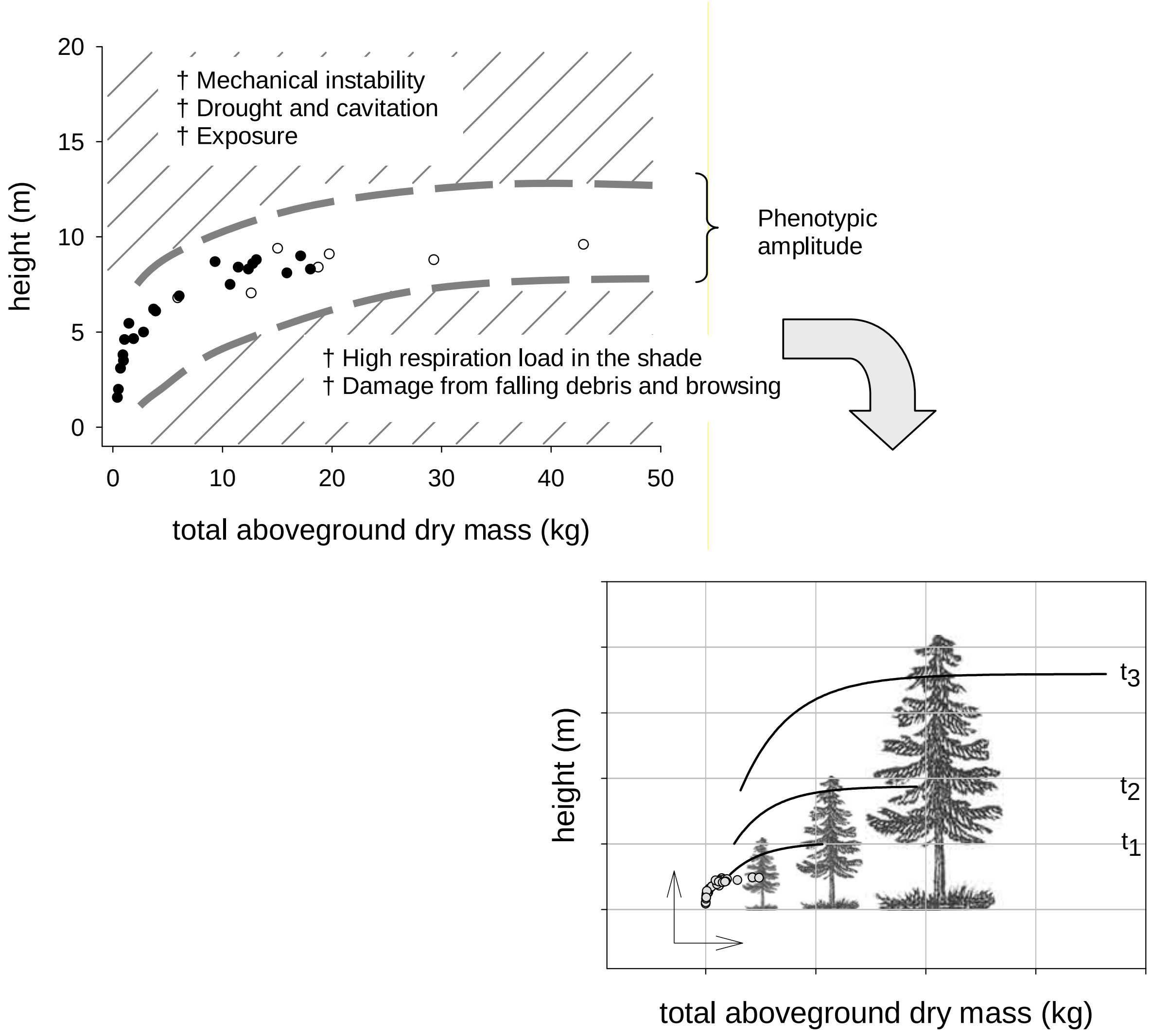


Fig. 7-1. Top figure: scatterplot of height in relation to biomass for saplings of Scots pine. The graph displays sampling data from multiple communities, recorded at a single moment in time (data from Chapter 3 and 4). Open and closed circles symbolize exposed and non-exposed crown positions respectively; dashed bold lines delineate different mortality probability regions. Bottom figure: a hypothetical temporal development of the datapoints in the top figure based on an increase in height (points move upward) and biomass (points move to the right). As the projected data are fictitious they are only outlined; t1 – t3 represent successive moments in time.

Species positions in an emergent stand structure

Different ontogenetic trajectories have an effect on stand structure, which can be seen as an emergent property of the morphology of the component species. Despite the young age of the sampled communities and the large range in sapling sizes in all species, we found a clear indication of (an ongoing) vertical stratification between species (Chapter 5). This was caused by differences in slenderness rather than time since establishment (i.e. age). More than just a population distribution of height-biomass values (Chapter 4), the data from Chapter 5 describe a single community, established in a period of about five years without species differences. These data show that over time species in fact developed along similar lines as the static sampling data previously suggested, further underlining the importance of a species' architecture.

Regardless of stratification, there was still a large overlap in heights between individuals of different species. It is likely that vertical stratification will continue as the overtopped individuals of light-demanding species will experience high mortality compared to more shade-tolerant species, while exposed individuals will outgrow these shade tolerants even further (Kitajima, 1994; Reich et al., 2003). This is supported by the crown class data, specifically the share of dominant individuals in Silver birch and Japanese larch, next to the large share of suppressed individuals in Scots pine and lack thereof in Douglas fir (Fig. 5-3). These results suggest that inherent ontogenetic trajectories have clear consequences for stand development. When individuals regenerate over a short period and subsequently develop according to their inherent species morphology, then over time a 'predictable' stand structure emerges in which particular species overtop others. This subsequently determines access to light, and ultimately the competitive relationships between species. Hence, the interspecific competition for light connects sapling ontogeny and community development. Growth responses to site quality differ between species, however, and this will also change competitive relationships and community development.

Interspecific competition for light

Species on average overtopped other species as a result of inherent growth patterns. The important question then is what this means for competitive relationships when growing together in a dense and mixed community. In the studied communities it turned out that rather than a competitive species *effect*, there was mostly a competitive species *response*. Both size differences and (to a lesser degree) neighbour tree species had a significant effect, but variation in relative crown depth (RCD) was explained far more by target species identity. This means that at this early point in stand development competitors are to a large extent equivalent and that only their size matters.

This apparent neighbourhood equivalence catches attention. Whether species are equivalent (cf. Hubbell, 2001) or, alternatively, they are not and species coexist through niche differentiation (cf. Kitajima and Poorter, in press) is an important current debate in ecology (Whitfield, 2002). However, going beyond such a strict dichotomy, many authors think that neutral processes (i.e. random dispersal and fluctuations in immigration, extinction and speciation) occur next to niche processes (based in *inter alia* competition, natural enemies, temporal and spatial variation in resources) and together determine community dynamics and structure (Gravel et al., 2006; Leibold and McPeek, 2006; Adler et al., 2007).
In our study we did not look at large ecosystems consisting of many species, and in which community structure is the result of the long-term effects of establishment, growth and mortality. We looked at naturally established saplings at the single community scale. Resulting from the limited temporal and spatial scale of the data, no robust inferences on the applicability of neutral theory can be made. Still, within the limits set by the experimental set up, we can conclude that in the competition for light in the studied gap assemblies competitor effects were largely neutral, that size differences between individuals were important, but that the most important factor was given by a species' sensitivity to light depravation.

These conclusions apply in relation to variation in the distribution of live foliage. Reduced crown depth, when not compensated for by a widening crown, implies a reduction in the amount of foliage. And with reduced foliage the whole-plant photosynthetic capacity is reduced, which in turn indicates a sapling's diminishing vitality (Oliver and Larson, 1996). The data from Chapter 5 showed a broad relationship between a sapling's crown position (CPI) and RCD. The correlation coefficient (Pearson's r) for Silver birch is 0.34 (n=64, p=0.003); for Douglas fir 0,54 (n=77, p<0.001); for Scots pine 0,51 (n=92, p<0.001); and for Japanese larch 0,26 (n=27, p=0.095). Despite the non-significance in larch, this correlation shows that individuals of higher CPI tend to have higher RCD as well, indicating their increased vitality through better access to light. How better access to light relates to long-term growth and mortality is, however, another matter which will be dealt with next.

The effects of light availability on growth and mortality

The four species we studied in gap assemblies tend to stratify in two storeys based on their growth patterns, with a top stratum formed by Silver birch and Japanese larch and a secondary stratum formed by Scots pine and Douglas fir, at least for the first few decades of stand development. In Chapter 6 we therefore analyzed the effect of crown position (CPI), a proxy for light availability (Jennings et al., 1999), on growth and mortality and how this differs between species.

Silver birch and Japanese larch showed their competitive ability by gaining dominant canopy positions after experiencing high initial growth. Scots pine was not able to do so. This species is overgrown even when experiencing good growth due to its low stem slenderness. The difference in light demand between species is shown by the growth data in relation to canopy position (Fig. 6-2). Silver birch, Japanese larch and Scots pine all showed reduced growth in response to the decreasing light levels in lower canopy positions. Overtopped individuals will therefore not survive in the shade. This is contrary to Douglas fir in which all individuals displayed a similar growth level independent of crown position.

Fully overtopped trees and trees that already had died showed a steady decline in growth leading up to death, irrespective of species, with sometimes highly erratic growth patterns. Two things catch the eye: first that the mortality probability curves do not differ significantly between Silver birch, Japanese larch and Douglas fir despite their wide range in light demand. And secondly, that the mortality probability curve for Scots pine indicates that there is no relation between growth level and mortality in this species, even though it is highly responsive to light. Next to the erratic growth patterns before death that we found in other species as well, these results suggest additional mortality agents at work in self-thinning next to the competition for light.

Species that differ in light demand are hypothesized to have different mortality curves, as displayed in Fig. 7-2 (Pacala et al., 1994; Kobe et al., 1995; Kobe and Coates, 1997). Light demanders are characterized by low persistence in the shade and high growth in full light. Shade tolerants on the other hand are characterized by high persistence in the shade, but do not reach high growth levels in full light. Low-light survival and high-light growth are therefore part of a trade-off, allowing light demanders and shade tolerants to coexist (Reich et al., 2003; Kitajima and Poorter, in press). In our case, however, we found more or less a single and thus common mortality probability curve.

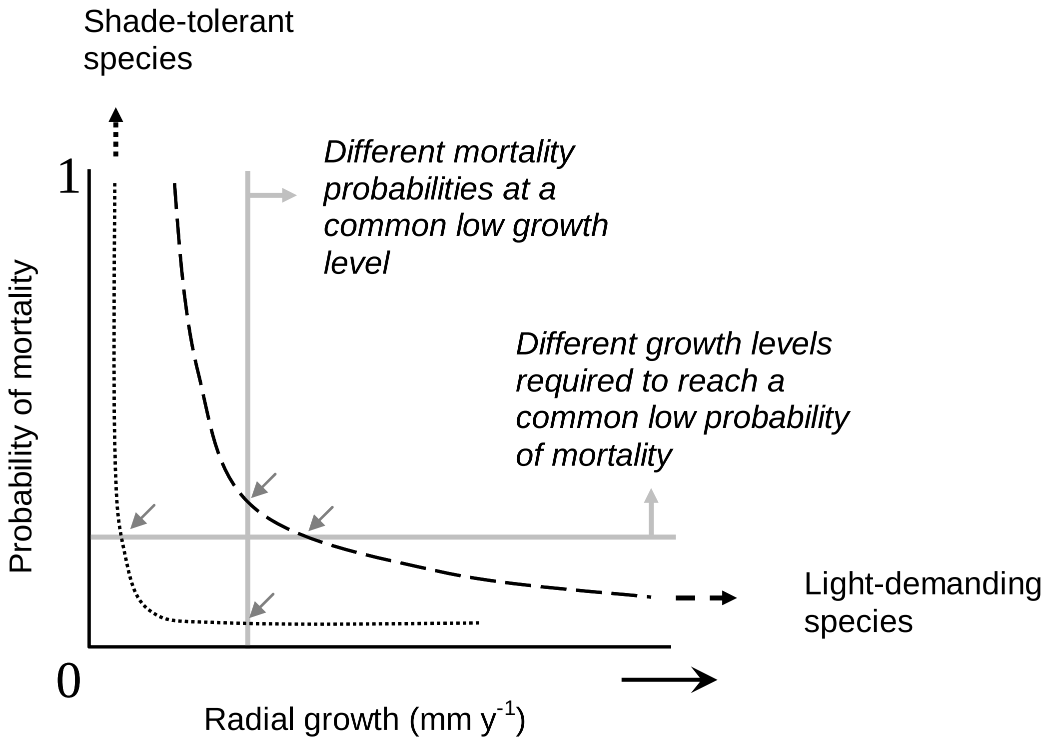


Fig. 7-2. A hypothetical relation between growth level and probability of mortality. The curvature indicates sensitivity to changes in light, the intercept indicates persistence to low growth

Despite the common mortality curve there is still niche partitioning in the studied communities. This niche partitioning is based in the different growth levels depending on crown position (i.e. light availability) and is illustrated in Fig. 7-3, and explained below.

Irrespective of CPI Douglas fir grew at an average of 2 mm radius y^{-1} (5-yr average). The other species only reached this growth level when growing in high light. Taking 2 mm radial growth as a reference growth level for interspecific comparison, then a 2 mm growth level (on a common, averaged mortality curve) is accompanied by a 5-yr mortality probability of at most 10 percent, or 2 percent per year.

Many individuals of Douglas fir, spread across all canopy positions, showed an average growth of at least 2 mm and will therefore likely survive the next few years. In contrast, only a small number of dominant individuals of Silver birch and Japanese larch displayed a growth of 2 mm or more. Only this small number has a high probability to survive the next few years, similar to Douglas fir. Overtopped and ill-performing individuals, however, will experience a growth reduction to around 1 mm radius y^{-1}. This growth level is accompanied by high mortality (up to 30 percent over 5 yrs, or 6 percent per year). A growth reduction additionally causes these individuals to become even more overtopped in a negative feedback loop.

Even though in Scots pine there was no direct relation between radial growth and probability of mortality, an estimate pointed to a high 5-yr mortality rate of nearly 40 percent. Despite its strong reaction to light availability, growth levels within both live and dead individuals were too variable for a significant relationship. The data still underline the results from previous chapters: Scots pine, in competition with the other species, is unable to keep up in height growth and slowly gets overtopped (on average that is). This does not depend on its radial growth level in high light, as this is equal to the other species. It does however result from its low height-diameter ratio that leads to short and stout stems, contrary to Silver birch and Japanese larch which invest in height extension. Its high light demand and low stature subsequently lead to high and stochastic mortality.
In time (the first few decades of stand development) these different mortality probabilities, in relation to the crown positions a species on average attains, can and likely will lead to the previously hypothesized two stratum stand in which light demanders (excluding Scots pine) form a layer overtopping the shade-tolerant Douglas fir, thus (at least temporarily) coexisting through a partitioning of the light gradient.

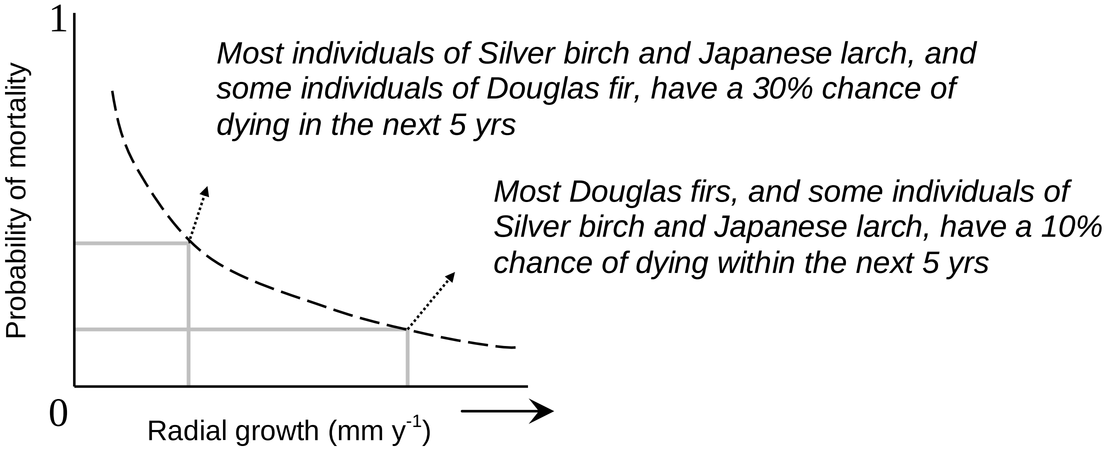


Fig. 7-3. A common mortality curve but with different species positions on it

Relevance of the results for close-to-nature silviculture in the Netherlands

The question remains what the previous findings mean for the coexistence of Silver birch, Douglas fir, Scots pine and Japanese larch in regeneration units, and what the application of close-to-nature silviculture could mean for forest management objectives like increasing tree species diversity.

The occurrence of Silver birch, Douglas fir, Scots pine and Japanese larch in the Netherlands

The focal species of this thesis are common in Dutch forests. In the most densely forested provinces (i.e. Drenthe, Overijssel, Gelderland, Limburg and

Noord-Brabant, together accounting for 76 percent of the Dutch forests), Silver birch, Douglas fir, Scots pine and Japanese larch are among the most abundant species growing on sandy soils. They occur in respectively 20 percent, 7 percent, 21 percent and 5 percent of 5,505 recorded plots in the national forest inventory (LNV, 2007). This inventory included the open, young and mature forest phases. Other important species are Pedunculate oak (*Quercus robur* L.), Sessile oak (*Quercus petraea* (Matt.) Liebl), Red oak (*Quercus rubra* L.), Spruce (*Picea abies* (L.) Karst) and European beech (*Fagus sylvatica* L.). When zooming in on young developmental phases (up to the pole stage), then the focal species are still among the most abundant species, both in occurrence in plots as well as total numbers (Fig. 7-5 C and D). A comparison between mature forest and young forest (compare Fig. 7-5 A-B with C-D) shows that abundant species are also abundantly present in the regeneration, without any clear shifts in species composition. What stands out most is an increase in Spruce and a decrease in Red oak in the national forest inventory.

To complement these data with a high resolution picture of tree species regeneration in the study area, gaps and other patches with natural regeneration have been inventoried in the Veluwe area. A total of 68 gaps in 38 stands from 6 management units were included in this study (Van der Loop, 2006). Silver birch, Douglas fir, Scots pine and Japanese larch were found in most recorded stands, and occurred in the highest densities of all recorded species (Fig. 7-5 E and F). These data show the importance of the four species of this thesis, especially on the dry and poor sandy soils in the Veluwe area of the Netherlands. They abundantly regenerate, but whether they can form sustainable species assemblages after gap-phase regeneration will be explored in the next sections.

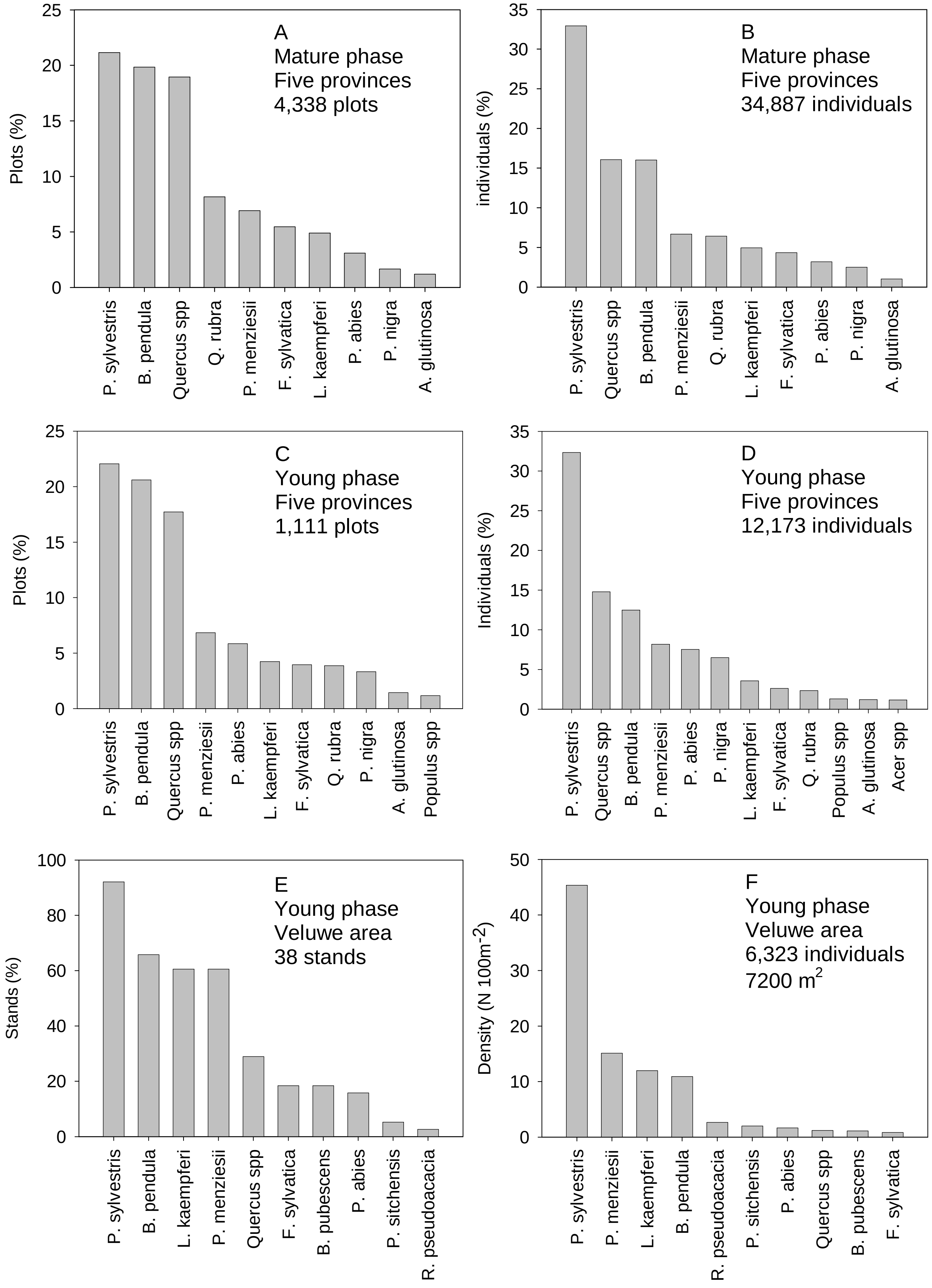

A
Mature phase
Five provinces
4,338 plots
Plots (%)
0
5
10
15
20
25
P. sylvestris
B. pendula
Quercus spp
Q. rubra
P. menziesii
F. sylvatica
L. kaempferi
P. abies
P. nigra
A. glutinosa
B
Mature phase
Five provinces
34,887 individuals
individuals (%)
0
5
10
15
20
25
30
35
P. sylvestris
Quercus spp
B. pendula
P. menziesii
Q. rubra
L. kaempferi
F. sylvatica
P. abies
P. nigra
A. glutinosa
C
Young phase
Five provinces
1,111 plots
Plots (%)
0
5
10
15
20
25
P. sylvestris
B. pendula
Quercus spp
P. menziesii
P. abies
L. kaempferi
F. sylvatica
Q. rubra
P. nigra
A. glutinosa
Populus spp
D
Young phase
Five provinces
12,173 individuals
Individuals (%)
0
5
10
15
20
25
30
35
P. sylvestris
Quercus spp
B. pendula
P. menziesii
P. abies
P. nigra
L. kaempferi
F. sylvatica
Q. rubra
Populus spp
A. glutinosa
Acer spp
E
Young phase
Veluwe area
38 stands
Stands (%)
0
20
40
60
80
100
P. sylvestris
B. pendula
L. kaempferi
P. menziesii
Quercus spp
F. sylvatica
B. pubescens
P. abies
P. sitchensis
R. pseudoacacia
F
Young phase
Veluwe area
6,323 individuals
7200 m^2
Density (N 100m^{-2})
0
10
20
30
40
50
P. sylvestris
P. menziesii
L. kaempferi
B. pendula
R. pseudoacacia
P. sitchensis
P. abies
Quercus spp
B. pubescens
F. sylvatica

Fig. 7-4 (previous page). Occurrence of the focal species in mature and young developmental phases (excluding the open phase). A, B, C and D are data from a nation-wide network of sample plots (LNV, 2007), E and F are from a large inventory of natural regeneration (Van der Loop, 2006). Only species are displayed that occurred in more than 1% of the plots or counts.
Fig. A: the focal species occur in 21, 20, 7 and 5 percent of 4,338 sample plots respectively. Fig. B: the focal species make up 33, 16, 7 and 5 percent of 34,887 recorded individuals. Fig. C: the focal species occur in 22, 21, 7 and 4 percent of 1,111 sample plots. Fig. D: the focal species make up 32, 13, 8 and 7 percent of 12,173 recorded individuals. Fig. E: the focal species occur in 92, 66, 61 and 61 percent of 38 inventoried stands. Fig. F: the focal species have densities of 45, 15, 12 and 11 individuals per 100m^2

Coexistence of the focal species after initial establishment

We showed that the crown positions of individuals (meaning their access to light) play an important role in competition and survival. Coexistence will then depend on the community distribution of crown positions. To illustrate, Fig. 7-5 displays cumulative frequency plots of crown positions for all four species from a single community (based on a total of 261 individuals, data from Chapter 5). Though these data stem from a single community, the data from Chapter 4 (cross-community data on height per unit biomass collected in a large area) support a wider generality of Fig. 7-5. In the graph grey dots indicate the cumulative population fraction at canopy positions ranging from being fully overtopped to being fully emergent (CPI 1-5). Arrows indicate the cumulative population fraction at CPI 3. The cumulative population fraction at this point contains all trees that are not dominant or emergent. For a part these trees are already overtopped (CPI 1-2), the remainder is closed in from all sides but not overtopped (CPI 3; see Clark and Clark, 1992). If CPI 3 trees cannot keep up with height growth as the community develops, they will be overtopped as well.

How the (short-term) coexistence of the focal species is influenced by the distribution of crown positions within the community, is best indicated by looking at two species of similar height growth but contrasting light demand: Douglas fir and Scots pine. These species are also the most abundant species (30 and 35 percent respectively, see legend to Fig. 7-5). About 20 percent of all Douglas firs are dominant individuals, leaving 80 percent that is overtopped or at risk from being overtopped. This species will mainly be restricted to a secondary stratum. Growth levels in Douglas fir are however independent of crown position and this species has a relatively low mortality. This means that a large fraction of the (abundant) Douglas fir population will survive (at least on the short term).

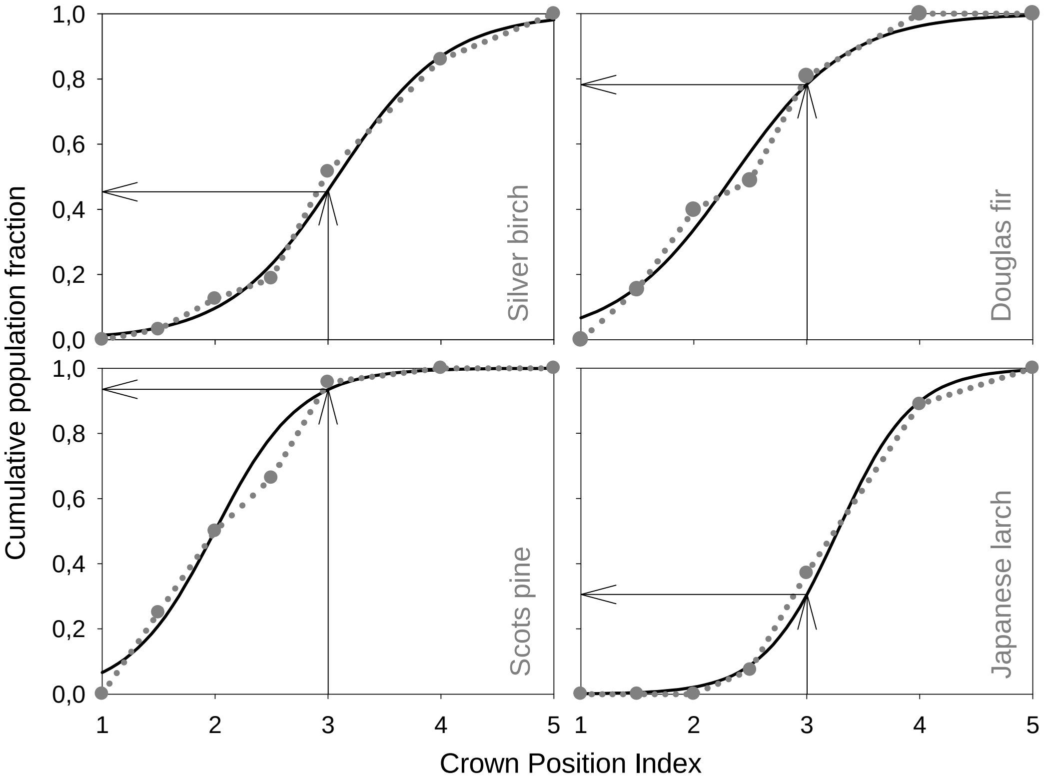


Fig. 7-5. Cumulative population fraction in relation to CPI (position of the crown in the canopy, including the intermediate values 1.5 and 2.5, see Clark and Clark, 1992). Logistic regression analysis on categorical data. Silver birch takes up ~25% of the total community, Douglas fir ~30%, Scots pine ~35% and Japanese larch ~10%. CPI values. The raw data are in grey, the regression line is displayed in black. Arrows indicate the population fraction that has a CPI between 1 and 3. Data from Chapter 5.

Scots pine, on the other hand, has only around 5 percent dominant individuals. This means that 95 percent is overtopped or at risk of becoming overtopped. Scots pine therefore similarly will be restricted to a secondary stratum. Resulting from its sensitivity to light depravation and high mortality, most of the overtopped individuals will die, now or in the future. As this involves 95 percent of the Scots pine population, these results suggests a future competitive displacement. This competitive displacement is driven by the general inability of Scots pine to gain sufficient access to light. Mortality subsequently results from long-term exhaustion, likely based in a combination of predisposing (e.g. light limitation), inciting (e.g. drought) and contributing (e.g. pathogens) stresses (cf. Manion, 1981). Hence, mortality appears stochastic. The fact that Scots pine cannot maintain itself in gap-phase competition is supported by its disappearance from closed forest conditions in the Atlanticum era, where it only persisted in stressed environments, e.g. harsh drought and low nutrient availability (Richardson and Rundel, 1998).

The other species, Silver birch and Japanese larch, will form a top stratum in the first decades of stand development. This is shown by the presence of large cohorts of dominant and emergent individuals summing up to 55 or 70 percent respectively of their populations (Fig. 7-5). The individuals that are (or will become) overtopped will die from lack of light, while the successful individuals will continue to overtop a large number of Douglas fir and a declining number of Scots pine. Given the lower abundances of birch and larch in the community, this top stratum will be a thin one. In time it will become even sparser from senescence and catastrophic mortality (e.g. windthrow). As the pines are declining, slowly Douglas fir will become more dominant as it is a species of high persistence that grows at a high mechanical safety margin.
Growth of individuals depends on environmental factors. Furthermore, species differ in their morphological adaptability, growth responses to nutrient rich (or poor) conditions, and their tolerance to lack (or surplus) of water. Additionally, these factors interact and influence mortality rates. As these are generally species-specific responses, growth patterns and how they relate to one another need not always be the same. Consequently, the emergent stand structure may also vary. The competitive displacement of Scots pine in the studied communities therefore does not imply that this species will always disappear from mixed-species assemblages. Under extreme site conditions (drought, low nutrient availability, high soil acidity), where other species will display stunted growth or high mortality, Scots pine may well be the strongest competitor. The community distribution of crown positions, resulting from the performance of all component species, will then show that under adverse conditions Scots pine does gain sufficient access to light in order to survive.

A competitive displacement of Scots pine and an increasing dominance of Douglas fir do not yet show in the species abundances in Fig. 7-4. Given sufficient time, such natural developments would become evident in differences between species abundance in the mature phase (mostly planted individuals) and the young phase (mostly naturally regenerated individuals). This however requires a natural species establishment and subsequent community development over a number of decades, without management intervention. The application of close-to-nature silviculture in the Netherlands, however, has not yet arrived at that point as (enrichment) planting and precommercial thinnings are still applied (cf. Van den Bos, 2002).

Expected future developments
Maximum height for Silver birch and Japanese larch lies between 27 and 30 meters (Jansen et al., 1996). In its native range Douglas fir can grow up to 80-100 meters tall, and additionally has a maximum life span of more than 600 years (CABI, 2005). In the Netherlands it grows outside its native range,

but this species can therefore potentially overtop Silver birch and Japanese larch as well as occupy a patch for a long time.

As soon as Douglas fir reaches 20 to 25 meters in height, which will take between 30 and 50 yrs depending on site quality, their crowns will begin to invade the top stratum and start competing for space and light. As it takes longer than three to five decades for birch and larch to reach their maximum height, in patches of natural regeneration this competition in the top stratum will start earlier. The dense crowns of Douglas fir will put the open and light-demanding crowns of Silver birch and Japanese larch at a disadvantage.

In the absence of active management intervention, patches of natural regeneration as described in the previous chapters will have converted back into a mature Douglas fir dominated forest within about a century. By then this species will be up to 40 m high, and the birches, pines and larches will mostly have died from senescence, competition and other causes like windthrow. The dense shade beneath the firs will not allow establishment of other trees except shade-tolerant (sub-canopy) species. As such species are uncommon in the Netherlands, in the long run tree species diversity would decline when gap phase regeneration with Douglas fir remains unmanaged. It is however unlikely to come to this as management interventions will take place well before this time.

Geïntegreerd bosbeheer advances the view to let natural regeneration develop unhindered for about 30 yrs. After self-thinning and self-pruning have taken their course, the forest manager can start selecting potential crop trees (PCTs) from the remaining individuals, and liberate them from competition (Van der Jagt et al., 2000; Van den Bos, 2002). By that time, there will be very few vital Scots pines left in the studied communities, there will be a number of dominant Silver birches and Japanese larches, and there will be a large cohort of Douglas firs. Irrespective of the particular selection of PCT trees, Douglas fir will therefore be a major component of the new forest stand. As the stand develops, this dense cohort of shade-tolerant Douglas firs will prevent the influx of other species. With limited seed sources of other species, Douglas fir will therefore have a tendency to become increasingly dominant, especially over multiple regeneration cycles. This is facilitated by a regular PCT system that identifies and liberates selected trees only, leaving the remaining stand to develop naturally. In the absence of a high natural disturbance regime or management interventions to regularly reduce numbers and open up the canopy, in the long run Douglas fir will most likely permanently displace Silver birch, Scots pine and Japanese larch, as well as other light demanding species. At this point, Douglas fir forest will not have diversified through close-to-nature management, but reverted back to Douglas fir forest. This clearly does not meet the objective to create a natural uneven-aged and mixed-species forest while producing quality timber.

To prevent ending up with a forest (stand) that is again dominated by a single exotic conifer, strong interventions are needed when the PCTs are liberated or harvested. Next to these regular PCT treatments, simultaneously growing space needs to be provided to other species. This can be achieved by cutting back Douglas fir, reducing its presence in mixed patches. In monospecific patches of Douglas fir, new ‘gaps’ with high-light conditions need to be created between and beneath the PCTs, exposing the mineral soil. This will allow other species to establish. Some monospecific patches can be left however, for example beneath a group of large Douglas fir PCTs. In this way a mosaic can be created where beneath the PCTs (of diverse species) some pockets of dense Douglas fir remain, next to areas of a more diverse species composition.

The combination of cutting back dominant individuals and creating new ‘gaps’ provides the opportunity for other species to establish, grow and reproduce in coexistence with Douglas fir. Scots pine however, being a species of extreme site conditions and primary succession environments, will still not survive under multi-species closed forest conditions.

Final remarks

This thesis focusses on conversion of monospecific Douglas fir plantations, which is a relevant and challenging case-study. Creating large gaps to be filled with natural regeneration does lead to a mixed species composition of both indigenous and broadleaved species. Results show however that allowing such communities to develop naturally for the first few decades, and then applying a regular PCT selection system, will likely lead to a loss of the diversity that was initially achieved. This results from strong Douglas fir regeneration, which is clearly to be expected in the studied communities. It nevertheless indicates that management activities have to be more intensive in challenging situations like the conversion of Douglas fir forest. Using natural processes and imitating ecosystem dynamics is therefore not synonymous with generating mixed, stable and productive forests. Autogenic processes do not always yield the desired forest characteristics. Depending on the starting conditions, in our case the massive presence of a highly competitive species, much more effort may have to be put in diversifying stands. It will not suffice to just create gaps, naturally regenerate, and let autogenic developments take their course. As regular and strong interventions may be needed, close-to-nature silviculture is not by definition cheaper to apply than other forms of management.

Other examples of potentially challenging situations are the nature-oriented conversion of monospecific Spruce or pine stands. Abundant species on sandy soils in the Netherlands are also abundantly present in regeneration (Fig. 7-4). This could mean that without strong interventions also monocultures of Spruce and pine will have a tendency to remain dominated by these species. Soil characteristics (like C/N ratio, soil acidity, seed bank composition, depth of the organic top layer) will not favour abundant regeneration of many species. Under such circumstances strong effort has to be made to sufficiently diversify these stands while reducing the numbers of Spruce and Pine.

This presents an ambivalent situation. Management has to make strong interventions counteracting the spontaneous development these stands would otherwise go through. The tendency in former Douglas fir plantations is to homogenise rather than diversify. The question is whether such active management intervention is a one-time correction of an initially disturbed condition, or is it the lengthy creation of a predefined and subjective image of natural forests?
There is no objective answer to this question. It remains subjective whether well structured and mixed-species stands of an exotic conifer can be considered natural, whether continued corrective management can be considered natural, or how natural the forest and its management need to be in order to be considered close-to-nature. What can be said is that society currently values certain forest characteristics, values which are based in the prevalent image of nature as a whole. The forests on which we project these values are the result of a historical management that was based in other values. Our forests therefore have to be adapted to meet societal demands, which is done by current management practices (irrespective of their exact name and origin). The question of naturalness is in fact superfluous. Of greater importance to their sustainable management is that our forests are valued in society, embedded in policy, and managed with care. As such, also more intensive application of *Geïntegreerd bosbeheer* agrees with the original idea behind close-to-nature silviculture: the creation of mixed, uneven-aged production forests to replace monospecific plantations under a clearcut system.

An interesting final question is what would happen if all forests were from now on indefinitely managed according to close-to-nature silviculture, i.e. *Geïntegreerd bosbeheer* with a regular PCT selection system? How would these forests develop?
Currently there is a great diversity of species at the landscape scale resulting from the (historical) planting of forests. Even though individual stands are often largely monospecific, there is an intimate mixture of stands of different species at larger spatial scales. This provides a rich seed source enabling a mixed species composition when new growing space becomes available. When gaps are created on a larger area and the ensuing regeneration is left for the first few decades, then species that have trouble surviving high-density high-competition closed forest situations (e.g. Scots pine, Pedunculate oak) in the end will give way to more competitive species (e.g. Douglas fir, Spruce). Without protective measures, and without a natural disturbance regime, shade-tolerant species like European beech, Douglas fir and Spruce will slowly gain ground. It is therefore probable that at least some of the initial diversity is lost in autogenic development of gap-phase regeneration, particularly over longer time scales. At the landscape

scale forests would therefore risk becoming more homogenous, especially when only PCTs are selected and at intervals liberated, and the remaining regeneration is left to spontaneous development.

If applying natural regeneration and using natural forest development would mean the absence of a repeated and active management that creates a diversity of stand types, then forests would homogenise. This is however improbable as forest management in the Netherlands has never entailed long term no-intervention management. Long term no-intervention management is not the intention in *Geïntegreerd bosbeheer* either. Undesirable developments have been and always will be corrected, whether explicitly incorporated as a policy objective or not.

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SUMMARY

Many planted monocultures in Europe now conflict with the societal demand for forests that should deliver multiple socio-economic and nature conservation values. In West-European forestry, including the Netherlands, the last decades the main focus has therefore shifted to uneven-aged mixed-species forests under close-to-nature management. This includes the transformation of even-aged single-species forests under a clearcut system. Natural regeneration in canopy gaps often forms the starting point for such transformation, and is meant to mimic natural ecosystem dynamics. After gap creation, seedlings will establish, grow and compete, and in the end will develop into the new mature cohort.

In order to assess possible consequences of the shift in management and the focus on autogenic processes, it is necessary to predict the community development of the species assemblages inside these canopy gaps.

This thesis presents data on sapling morphology, competition, growth and mortality in gap-phase regeneration. Data were collected on four species in naturally regenerated canopy gaps in Douglas fir forest which were to be converted into multi-species stands. Focal species of this thesis are Silver birch (*Betula pendula* Roth.), Japanese larch (*Larix kaempferi* Carr.), Scots pine (*Pinus sylvestris* L.) and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco). These species dominate natural regeneration in gaps in Douglas fir forest. This study was carried out in forests on dry sandy soils in the Veluwe area of the Netherlands, but biomass sampling took place over a wider area. The recorded gaps were created as part of the nature-oriented conversion of monospecific plantations.

The overall aims of this study were: 1) to investigate the international socio-political framework for close-to-nature silviculture; 2) to evaluate species performance in mixed-species sapling communities. With species performance is meant the ability of a species to maintain itself, i.e. to grow, to compete, and to persist in mixture with other species; and 3) to explore the implications of this performance for the long-term coexistence of species. More specifically, this thesis tests whether, after the application of gap-phase regeneration and in the stem exclusion phase, species stratify in height and in doing so reach a situation of niche differentiation that promotes their coexistence. By taking basic plant traits such as height per unit biomass and emerging community traits like vertical stratification, and by connecting this to the competition for light in the self-thinning phase, this work infers consequences for stand development and species coexistence.

Contemporary forest management objectives

Today, there is a large share of even-aged and monospecific forest in Europe resulting from the historical establishment of plantations. The current view on sustainable forest management however, calls for multifunctional forests that take both ecological and economical factors into account and that are valuable to society. In this view, forest management should work with ecosystem dynamics, and imitate natural disturbances.

This discrepancy calls for a reorientation on more ‘ecological’ forms of forest management. In international forest policies this is referred to as Ecosystem Management, but many semi-synonymous terms exist side by side. At the international level, policy documents are in general agreement in suggesting a focus on intrinsic non-use values, socio-economic aspects and ecosystem complexity.

When putting Ecosystem Management into practice, then the methods from close-to-nature silviculture are applied. This is sometimes referred to as a ‘back to nature’ approach, and the goal is to create multi-functional forests in which 1) natural processes like regeneration and succession are allowed to take place; 2) practices are used that mimic or utilize natural dynamics; 3) there is no room for intensively managed monocultures; 4) there is a mixed, indigenous species composition; and 5) there is an uneven-aged forest structure.

Forest policies therefore advocate a forest management that allows natural cycles to take their course, and that produces quality timber at the same time. Close-to-nature silviculture is subsequently applied with the objective to create the desired uneven-aged and mixed-species forests.

Growth patterns and vertical stratification in the gap building phase

Saplings enter the self-thinning phase in the first decades after their establishment in newly created canopy gaps. High mortality during this phase will affect species composition of the regeneration unit as it continues to develop.

Morphology is an important factor in self-thinning. Growing tall and thin leads to less competition for space with neighbours, and additionally allows an individual to overtop others. Being short and wide on the other hand, leads to stronger competition for space but yields higher mechanical safety. These two extremes are generally associated with light-demanding and shade-tolerant strategies respectively.

The focal species of this thesis differed in their achieved height per unit biomass. Silver birch and Japanese larch were taller for a given DBH or amount of biomass than Scots pine or Douglas fir. This divergence was caused by differences in biomass partitioning and (stem) slenderness. Together, these factors strongly determined mass-based heights. A high stem biomass fraction combined with high stem slenderness led to tall trees, and a low stem biomass fraction with low stem slenderness led to short trees. This was however unrelated to light demand as the pioneer Scots pine was among the shortest species.

Differences in mass-based height started already early and grew stronger with increasing size, leading to distinct growth patterns that were independent of crown position and sapling age. When growing in a single community, established within a period five years, these growth patterns enabled Silver birch and Japanese larch to overtop Scots pine or Douglas fir. Even though heights of all species still overlapped, there was already a vertical stratification in the community. This was indicated by the average crown positions of species. That this stratification is likely to grow stronger, can be seen in the large share of suppressed individuals in Scots pine and the lack thereof in Douglas fir, next to the many dominant individuals in Silver birch and Japanese larch.

The competition for light

A consequence of the vertical stratification of tree crowns is that this influences access to light and, as one species overtops another, competitive relationships. To evaluate the interspecific competition for light, the effect on a target tree was quantified by size, foliage mass and species of a neighbour tree. The response variable was relative crown depth, a proxy for the amount of live foliage.

Results demonstrate a competitive species response of the target tree, rather than a competitive species effect by the neighbor tree. Size, foliage mass and (to a lesser degree) neighbour tree species had a significant effect, but these were small in comparison to the effect of target species identity. This means that in the sapling phase of early stand development competitors are to a large extent equivalent, that size differences between individuals are important, but that the most important factor in the competition for light in the sapling phase is given by a species' sensitivity to light depravation.

The effect of access to light on growth and mortality

The results on the interspecific competition for light make a connection between the canopy position of a tree (its height relative to the surrounding canopy and hence a proxy for access to light) and its crown depth. A reduced crown depth implies a reduction in the amount of foliage. This in turn leads to reduced photosynthetic capacity and points to a diminishing vitality, as was found earlier for the often overtopped Scots pine. Since a species' sensitivity to light depravation was the strongest factor in the competition for light, the effect of a tree's canopy position on radial growth was assessed, next to the effect of growth on the probability of mortality. Growing under high-light conditions had a marked effect on radial growth levels in Silver birch and Japanese larch. Initial high growth as a seedling enabled these species to gain dominant canopy positions later on. Scots pine responded similarly to high light but was not able to gain a dominant canopy position, even when experiencing high growth as a seedling. In Douglas fir there was no effect of access to light on radial growth.

The probability of mortality in Silver birch, Japanese larch and Douglas fir depended on radial growth. This probability was however the same for all species, despite their differences in light demand. Even though species had similar mortality probability curves, their species-specific canopy positions place them on different positions on this common mortality curve. This allows a partitioning of the light gradient, at least on the short term.

Scots pine showed no relationship between growth and the probability of mortality, but was nevertheless characterized by high mortality. Its low slenderness lead to short and stout stems, and as a result this species was unable to keep up in height growth. Its high light demand and low stature subsequently lead to a high and stochastic mortality, likely in combination with inciting and contributing factors.

The results on Silver birch, Japanese larch and Douglas fir fit within the framework of a growth-survival trade-off, and allow niche partitioning and coexistence. The results on Scots pine do not fit within such a framework as it cannot maintain a canopy position, even in high light. This emphasizes the importance of height growth (or alternatively shade tolerance), and points towards the competitive displacement of Scots pine from high-density high-competition gap communities.

Implications for forest management

Silver birch, Japanese larch, Scots pine and Douglas fir are abundant species in the Netherlands, especially in regenerating communities in the Veluwe area. How these species will develop inside regeneration units can be evaluated by looking at the community distribution of crown positions in relation to the growth and mortality resulting from these positions. Such an approach revealed that most Scots pines in the population are (or eventually will be) overtopped. This species will experience a growth reduction and high mortality, and will be competitively displaced. Silver birch and Japanese larch both have a large number of dominant individuals that will survive to form a low-density top stratum. The unsuccessful individuals in the understory will experience high mortality. Douglas fir on the other hand shows high survival in the understory and will become increasingly dominant over time.

Under a Potential Crop Tree (PCT) selection system that apart from liberating PCTs (even when these are from other species than Douglas fir) allows the spontaneous development of the remaining stand, these mixed communities will eventually revert back to Douglas fir forest. This will happen especially when a PCT selection system is in place over multiple regeneration cycles. This does not agree with the objective to create mixed-species forests. To maintain species diversity, stronger interventions are necessary to reduce the presence of Douglas fir and create the circumstances that enable species diversity. This does not however fall outside of a close-to-nature approach, which does not exclude active management interventions.

SAMENVATTING

Veel van de aangeplante monocultures in Europa zijn in strijd met de huidige maatschappelijke vraag naar multifunctionele bossen met hogere natuurwaarden. In West-Europa, inclusief Nederland, is er dan ook toenemende aandacht voor een natuurvolgende bosbouw gericht op ongelijkjarige en gemengde bossen. Hier valt ook de omvorming van gelijkjarige monocultures onder. Als startpunt voor omvorming wordt vaak natuurlijke verjonging toegepast in kronendakgaten, een nabootsing van de dynamiek in natuurlijke ecosystemen. Na het ontstaan van een gat in het kronendak zal natuurlijke verjonging zich vestigen, zich ontwikkelen, en zullen de individuen concurreren om deel uit te maken van het toekomstige, volgroeide bos.
Om de gevolgen van het natuurvolgende bosbeheer met zijn nadruk op natuurlijk verlopende processen in te kunnen schatten, is het nodig om te voorspellen hoe de soortensamenstelling in deze kronendakgaten zich zal ontwikkelen.

Dit proefschrift gaat in op morphologie, concurrentie, groei en mortaliteit in natuurlijke verjonging in kronendakgaten. Van vier soorten zijn gegevens verzameld in kronendakgaten in Douglas bossen onder omvormingsbeheer naar gemengd bos. Deze soorten zijn Ruwe berk (*Betula pendula* Roth.), Japanse lariks (*Larix kaempferi* Carr.), Grove den (*Pinus sylvestris* L.) en Douglasspar (*Pseudotsuga menziesii* Mirb. Franco). Deze soorten domineren de natuurlijke verjonging in Douglas bos. Het veldwerk voor dit proefschrift is uitgevoerd op de droge zandgronden van de Veluwe, maar het verzamelen van biomassagegevens vond plaats in een groter gebied. Alle bezochte kronendakgaten zijn gecreëerd in het kader van de natuurgerichte omvorming van gelijkjarige monocultures.

Het drieledige doel van dit werk was: 1) het achterhalen van het internationale sociaal-politieke raamwerk voor natuurvolgende bosbouw; 2) het onderzoeken van de ontwikkeling van soorten in gemengde natuurlijke verjongingen. Ontwikkeling betreft dan het vermogen van soorten om te groeien, te concurreren en zich te handhaven in menging; en 3) het verkennen van de implicaties van deze ontwikkeling op de coexistentie van de onderzochte soorten. In specifieke termen, dit proefschrift onderzoekt of er in de zelfdunningsfase binnen natuurlijke verjongingen een verticale stratificatie optreedt, en of er zo niches gecreëerd worden die coexistentie mogelijk maken. Door uit te gaan van basale soortseigenschappen als de hoogte per eenheid biomassa en de gevolgen daarvan op verticale stratificatie, en door dit de koppelen aan de concurrentie om licht in de zelfdunningsfase, wil dit werk de gevolgen duidelijk maken voor opstandsontwikkeling en coexistentie.

Doelstellingen in het hedendaags bosbeheer

Het Europese bos kent een groot aandeel gelijkjarige monocultures als gevolg van de grootschalige aanplant ervan in het verleden. De moderne kijk op duurzaam bosbeheer vraagt echter om bossen waarin zowel de economische als de ecologische waarde van het bos een rol speelt. Bossen die gewaardeerd worden in de maaschappij, die gebruik maken van natuurlijke dynamiek, en deze ook nabootsen.

Deze discrepantie leidt tot een heroriëntatie op meer 'natuurlijke' vormen van bosbeheer. In internationale beleidsdocumenten wordt dit Ecosysteem Beheer genoemd, maar hier bestaan vele quasi-synonieme termen voor. Op internationaal niveau roept het beleid er eensluidend toe op om rekening te houden met intrinsieke natuurwaarden los van het gebruik van het bos, met sociaal-economische aspecten van bosbeheer, en met de inherente complexiteit van ecosystemen.

Wanneer Ecosysteem Beheer in de praktijk wordt gebracht, worden de methoden van natuurvolgend bosbeheer gebruikt. Dit wordt ook wel een 'terug naar de natuur' aanpak genoemd, en het doel is om multifunctionele bossen te creëren waarin 1) natuurlijke processen zoals regeneratie en successie plaatsvinden; 2) het bosbeheer de natuurlijke dynamiek benut en nabootst; 3) er geen vlaktegewijs kaalkapbeheer van monocultures plaatsvindt; 4) een gemengde inheemse soortensamenstelling nagestreefd wordt; en 5) een ongelijkjarige bosstructuur gecreëerd wordt.

Het bosbeleid staat derhalve een bosbeheer voor gebaseerd op natuurlijke processen, en dat tegelijkertijd kwaliteitshout produceert. Natuurvolgend bosbeheer wordt vervolgens toegepast om de gewenste gemengde, ongelijkjarige bossen te creëren.

Groeipatronen en verticale stratificatie in de jonge-, dichte- en stakenfase

In de eerste tientallen jaren na de vestiging van natuurlijke verjonging in een kronendakgat, treedt de zelfdunningsfase op. De hoge sterfte die optreedt gedurende deze fase heeft een sterke invloed op de soortensamenstelling van de regeneratie.

Morphologie is een belangrijke determinant van zelfdunning. Door lang en slank te groeien vermijdt een individu de concurrentie om ruimte met zijn buren, en dit stelt hem tegeijkertijd in staat om boven anderen uit te groeien. Een korte en robuuste bouw leidt tot meer concurrentie om ruimte, maar is daarentegen veiliger uit mechanisch oogpunt. Deze extremen worden veelal geassocieerd met lichtbehoevende- en schaduwverdragende strategieën.

De vier soorten van dit proefschrift verschilden in hun hoogte per eenheid biomassa. Ruwe berk en Japanse lariks waren hoger dan Grove den en Douglas voor een gegeven DBH of biomassa. Deze uiteenlopende boomhoogten werden veroorzaakt door verschillen in biomassaverdeling en slankheidsgraad van de stam. Een hoge biomassafractie in de stam, gecombineerd met een hoge slankheidsgraad, leidde tot hoge bomen. Een lage biomassafractie in de stam, gecombineerd met een lage

slankheidsgraad, leidde tot lage bomen. Dit was echter onafhankelijk van lichtbehoevendheid. Dit werd aangetoond door Grove den die als pioniersoort toch tot de laagste soorten behoorde.
De verschillen in hoogte per eenheid biomassa manifesteerden zich al vroeg en werden sterker bij toenemende boomgrootte. Dit uitte zich in onderscheidbare groeipatronen die onafhankelijk waren van kroonpositie of leeftijd. In een gelijkjarige regeneratie-eenheid, gevestigd binnen een periode van vijf jaar, gaven deze groeipatronen aan Ruwe berk en Japanse lariks de gelegenheid om boven Grove den en Douglas uit te groeien. Zelfs al was er nog veel overlap in boomhoogten tussen soorten, toch was er al een verticale stratificatie zichtbaar in de regeneratie-eenheid. Dit werd aangetoond door de gemiddelde kroonpositie per soort. Deze stratificatie zal sterker worden met de tijd. Dit is zichtbaar in het grote aandeel onderdrukte individuen in Grove den en het gebrek hieraan in Douglas, in combinatie met de vele dominante individuen in Ruwe berk en Japanse lariks.

De concurrentie om licht

Een gevolg van verticale stratificatie is dat het de lichtbeschikbaarheid beïnvloedt en, omdat de ene soort de ander overtopt, ook concurrentieverhoudingen. Concurrentieverhoudingen zijn onderzocht door het effect op een doelboom van soort, grootte en bladmassa van een buurboom te kwantificeren. De responsvariabele was de relatieve kroondiepte, een maat voor de hoeveelheid levende bladmassa.
De resultaten laten een competitieve respons zien van de doelboom, in plaats van een competitief effect van de buurboom. Grootte, bladmassa en (in mindere mate) soort hadden een significant effect, maar dit effect was klein ten opzichte van de soortspecifieke respons van de doelboom. Dit duidt erop dat in de dichte- en stakenfase concurrenten gelijkwaardig zijn, dat de grootte van een concurrent wel belangrijk is, en dat de belangrijkste factor in de concurrentie om licht in deze vroege ontwikkelingsfase de soortspecifieke gevoeligheid is voor lichtgebrek.

Het effect van lichtbeschikbaarheid op groei en mortaliteit

De resultaten van het onderzoek naar de concurrentie om licht leggen een verband tussen de kroonpositie van een boom (zijn hoogte in verhouding tot het kronendak en daarmee een schatter voor lichtbeschikbaarheid) en zijn kroondiepte. Een afnemende kroondiepte wijst op een vermindering van de hoeveelheid bladmassa. Dit wijst weer op een verminderde fotosynthetische capaciteit, wat leidt tot een lagere vitaliteit. Deze verminderde vitaliteit was eerder al gevonden voor de veelal overtopte Grove den. Omdat de soortspecifieke respons de belangrijkste factor was in de concurrentie om licht, zijn het effect van kroonpositie op diametergroei en het effect van groei op sterftekans onderzocht.
Als de kroon veel licht ontving, dan had dit een duidelijk effect op diametergroei in Ruwe berk en Japanse lariks. Een hoge groeisnelheid als

zaailing leverde deze soorten later een dominante kroonpositie op. Grove den reageerde ook met een sterke diametergroei op veel licht, maar deze soort was niet in staat om een dominante kroonpositie te verwerven. Ook niet na snelle jeugdgroei. Douglas vertoonde geen enkele reactie op lichtbeschikbaarheid.

De sterftekans van individuen van Ruwe berk, Japanse lariks en Douglas was afhankelijk van diametergroei. Deze kans verschilde echter niet tussen soorten, ondanks hun verschillende lichtbehoevendheid. Soorten bevinden zich niettemin op verschillende posities op de gemeenschappelijke mortaliteitscurve dankzij de verschillende kroonposities (en dus groeiniveaus) die soorten gemiddeld behalen. Dit maakt een scheiding van soorten in niches mogelijk, in ieder geval op de korte termijn.

Grove den vertoonde geen relatie tussen groei en sterftekans, maar kende niettemin een hoge mortaliteit. Zijn lage slankheidsgraad, en daarmee korte en robuuste stam, betekende dat hij niet in staat was mee te komen in hoogtegroei. Zijn hoge lichtbehoevendheid en lage kroonpositie leidde tot een hoge maar stochastische mortaliteit. Deze mortaliteit trad waarschijnlijk op in combinatie met andere, aanvullende factoren.

De resultaten met betrekking tot Ruwe berk, Japanse lariks en Douglas passen binnen een trade-off tussen groei en overleving, en staan een scheiding in niches en daarmee coexistentie toe. De resultaten met betrekking tot Grove den passen niet binnen dit raamwerk aangezien deze soort niet in staat is om een positie in het kronendak te verwerven, zelfs niet bij goede groei. Dit benadrukt het belang van hoogtegroei (of schaduwtolerantie), en suggereert de competitieve uitsluiting van Grove den in dichte gemengde verjongingen waar sterk geconcurreerd wordt om licht.

Implicaties voor het bosbeheer

Ruwe berk, Japanse lariks, Grove den en Douglas komen veel voor in het Nederlandse bos, vooral in de natuurlijke regeneratie op de Veluwe. Hoe deze soorten zich zullen ontwikkelen kan worden ingeschat door te kijken naar de verdeling van kroonposities binnen dergelijke regeneratie-eenheden. Dit kan dan gerelateerd worden aan de groei en sterftekans die samenhangt met deze kroonposities. Zo’n aanpak toont aan dat de meeste Grove dennen zijn of worden overtopt. Deze soort zal daarom een groeireductie en hiermee samenhangende hoge mortaliteit laten zien. Uiteindelijk zal deze soort worden weggeconcurreerd. Ruwe berk en Japanse lariks hebben beiden een groot aandeel dominante individuen. Deze zullen voor het grootste deel overleven en uiteindelijk een dunne bovenlaag vormen. De kleinere individuen in de onderlaag zullen slecht groeien en een hoge mortaliteit kennen. Douglas daarentegen, die ook in de onderlaag groeit, laat een hoge overleving zien en zal in de loop der tijd steeds dominanter worden.

Onder een systeem van toekomstbomendunning (ongeacht of dit een andere soort is dan Douglas) met natuurlijke ontwikkeling van de overige opstand zullen regeneratie-eenheden van deze vier soorten uiteindelijk weer gewoon Douglas bos worden. Dit effect zal sterker zijn als zo’n systeem over meerdere regeneratiecycli wordt toegepast. Dit staat haaks op de doelstelling om gemengde bossen te creëren. Om de soortsdiversiteit te handhaven zullen sterkere ingrepen nodig zijn die Douglas terugdringen en tegelijk die omstandigheden creëren die soortsdiversiteit mogelijk maken. Zulk ingrijpen valt echter niet buiten de doelstelling van natuurvolgend bosbeheer.

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CURRICULUM VITAE

Marco Dekker was born on August 26, 1971 in Koog aan de Zaan, but soon after he moved to Amsterdam. After first finishing the MAVO (Lower General Secondary Education) he went on to do the HAVO (Higher General Secondary Education), and finally received his VWO (pre-university) diploma in 1991. After this a period followed of doing temporary jobs, as well as a year of studying Philosophy at the Free University of Amsterdam. After again a period of temporary jobs, he started his MSc study Forest and Nature Conservation in 1996 at Wageningen University.

During his MSc study he mostly focussed on forest ecology and research methodology. For his first MSc thesis he went to the Celos institute in Suriname to do a field study in the tropical rainforest. In this study he investigated regeneration patterns after logging. For his second MSc thesis he chose a different approach and carried out model simulations using the CO2FIX model. This time he investigated carbon sequestration in Mexican temperate forests.

Next to studying, he functioned as treasurer for the Students Committee for Forest and Nature Conservation Students (WSBV). He also was a student member of the Faculty Educational Committee (ROC), as well as the Faculty Committee for Educational Reform (BSc/MSc Project Team). Additionally, he regularly helped out as a student-assistant in courses and practicals.

After graduation in 2002 he started as a PhD student at the Forest Ecology and Forest Management Group of Wageningen University. In this position he took part in the EU Silvistrat Consortium. This consortium was formed by European research groups, and studied and developed adaptive management strategies for sustainable forest management in European forests under scenarios of global climate change. Next to his work for Silvistrat, he developed his own research on close-to-nature silviculture of which the current thesis is the result.

While writing his dissertation, he started working in 2007 for the Dutch Ministry of Agriculture, Nature and Food Quality as project coordinator within the NATURA 2000 project. After completion of this project he started working full time for the research and consultancy firm that he founded together with a friend from university.

PUBLICATIONS

Published in peer reviewed journals:

Dekker, M., Verkerk, P.J., and Den Ouden J. 2008. Target species identity is more important than neighbor species identity. Forest Ecology and Management, Vol 255: 203–213.

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PE&RC PHD EDUCATION CERTIFICATE

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 ECTS)

- Global, European and national environmental policies (work done for the Silvistrat project) (2002-2003)

Post-Graduate Courses (7.0 ECTS)

- Basic and advanced statistics; PE&RC (2003)
- Multivariate analysis; PE&RC (2004)
- Spatial and temporal scales in resource ecology; PE&RC (2005)
- Survival analysis; PE&RC (2005)

Competence Strengthening / Skills Courses (4.2 ECTS)

- Career perspectives; PE&RC (2005)
- Competence assessment; PE&RC (2005)
- The art of writing; CENTA (2005)

Discussion Groups / Local Seminars and Other Scientific Meetings (7.0 ECTS)

- Discussion group Production Ecology and Resource Conservation (2002-2006)
- Weekly chair group scientific meetings and presentations (2002-2006)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.2 ECTS)

- PE&RC day (2002)
- PE&RC day (2003)
- PE&RC day (2004)
- PE&RC day (2005)

International Symposia, Workshops and Conferences (7.0ECTS)

- International Silvistrat project meetings / workshops (2002-2004)
- Conference Forest History and Biodiversity; Katholieke Universiteit Leuven (2004)

Course in which the PhD Candidate Has Worked as a Teacher

- Trends in Forest and Nature Conservation (2003); FEM, 2 days
- Models for Forest and Nature Conservation (2003); FEM, 7 days
- Academic Master Cluster (2005); FEM, 7 days
- Practical Forest Ecology and Management (2005); FEM, 1 day