

EFORWOOD
Tools for Sustainability Impact Assessment

Forest stands management and vulnerability to biotic and abiotic hazards

Jactel, H., Branco, M., Gonzalez-Olabarria, J.R., Grodzki, W., Långström, B.,
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Preface

This report is a deliverable from the EU FP6 Integrated Project EFORWOOD – Tools for Sustainability Impact Assessment of the Forestry-Wood Chain. The main objective of EFORWOOD was to develop a tool for Sustainability Impact Assessment (SIA) of Forestry-Wood Chains (FWC) at various scales of geographic area and time perspective. A FWC is determined by economic, ecological, technical, political and social factors, and consists of a number of interconnected processes, from forest regeneration to the end-of-life scenarios of wood-based products. EFORWOOD produced, as an output, a tool, which allows for analysis of sustainability impacts of existing and future FWCs.

The European Forest Institute (EFI) kindly offered the EFORWOOD project consortium to publish relevant deliverables from the project in EFI Technical Reports. The reports published here are project deliverables/results produced over time during the fifty-two months (2005–2010) project period. The reports have not always been subject to a thorough review process and many of them are in the process of, or will be reworked into journal articles, etc. for publication elsewhere. Some of them are just published as a “front-page”, the reason being that they might contain restricted information. In case you are interested in one of these reports you may contact the corresponding organisation highlighted on the cover page.

Uppsala in November 2010

Kaj Rosén

EFORWOOD coordinator

The Forestry Research Institute of Sweden (Skogforsk)

Uppsala Science Park

SE-751 83 Uppsala

E-mail: firstname.lastname@skogforsk.se



EFORWOOD
Sustainability Impact Assessment
of the Forestry - Wood Chain



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D 2.4.3 – Forest stands management and vulnerability to biotic and abiotic hazards

Jactel¹, H., Branco², M., Gonzalez-Olabarria^{3, 4}, J.R., Grodzki⁵, W., Långström⁶, B., Moreira⁷, F., Netherer⁸, S., Nicoll⁹, B.C, Orazio^{1, 10, 11}, C., Piou¹², D., Santos², H., Schelhaas¹³, M.J., Tojic¹⁴, K., Vodde¹, F.,

¹ – INRA, UMR 1202, Biodiversity, Genes & Communities, Laboratory of Forest Entomology & Biodiversity, F-33610 Cestas, France.

² – Centro de Estudos Florestais, Instituto Superior Agronomia, Universidade Técnica de Lisboa. Tapada da Ajuda, 1349-017 Lisboa, Portugal

³ – Centre Tecnològic Forestal de Catalunya; Pujada del Seminari s/n E-25280 Solsona, Lleida, Spain

⁴ – Mediterranean Regional Office – EFIMED, European Forest Institute, Spain

⁵ – Forest Research Institute, Department of Forest Management in Mountain Regions, ul. Fredry 39, 30-605 Kraków, Poland.

⁶ – The Swedish University of Agricultural Sciences, Department of Entomology, P.O. Box 7044, S-750 07 Uppsala, Sweden

⁷ – Centro de Ecologia Aplicada “Prof. Baeta Neves”, Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal

⁸ – University of Natural Resources and Applied Life Sciences, Department of Forest and Soil Sciences, Institute of Forest Entomology, Forest Pathology, and Forest Protection, Hasenauerstrasse 38, A-1190 Vienna, Austria.

⁹ – Forest Research, Northern Research Station, Roslin, Midlothian, Scotland, UK EH25 9SY, United Kingdom.

¹⁰ – FCBA, Domaine de Sivaillan Les Lamberts 33480 Moulis en Médoc, France

¹¹ – IEFC, 69, route d’Arcachon, 33612 Cestas, France

¹² – Département de la Santé des Forêts, Ministère de l’Agriculture et de la Pêche, Impasse R. Lavigne 33150 Cenon France

¹³ – Centre for Ecosystem Studies, Alterra, Wageningen UR, PO Box 47, NL-6700 AA Wageningen, the Netherlands

¹⁴ – Albert-Ludwigs-University Freiburg, Institute for Forest Growth, Tennenbacher Str. 4, 79106 Freiburg, Germany.

Abstract

We have synthesized and reviewed the available information of the effects of forestry practices on stand vulnerability to biotic and abiotic hazards in European forests, concentrating on mammal herbivores, pest insects, pathogenic fungi, wind and fire.

Site selection plays a major role in the future vulnerability of newly established forest stands to disturbance agents. The most important site characteristics are topography and related thermal conditions which influence wind action and development of biotic hazards, and soil properties which influence the physiological resistance of trees against damaging agents.

Site preparation may affect the risks to forest health in both positive and negative ways, depending on the type of application and the type of risk. A positive effect is obtained via the reduction of breeding material and fuel by the management of cutting residues. No general recommendation concerning fertilization can be given since the results of experiments appear contradictory, with both positive and negative effects.

Tree species diversity can have various effects on ecosystem processes and stability against disturbances, but generally mixed forests are expected to be more resistant to biotic agents than pure stands. In particular mixed forests would be less prone to outbreaks of specialist species (developing on a limited number of related tree species) of herbivorous mammals, insects and pathogenic fungi due to lower resource availability and higher impact of natural enemies. The picture is less clear for generalist species of damaging agents. Depending on the composition of tree species, some mixtures would be also more resistant to strong winds and fire.

Tree genotypes have been found to vary in susceptibility to biotic, and to a lesser extent to abiotic, damaging agents, presenting the opportunity for breeding programs to improve tree resistance. However the most relevant characteristics are often difficult to detect and select, they are sometimes negatively correlated to other selection criteria such as growth or shape and the genotype \times environment interaction may reduce their expression. Also, extended use of improved tree varieties may lead to adaptation by insect pests or pathogenic fungi. It is because of these limitations that few breeding programs for tree resistance have been developed in Europe, and why tolerance is more often targeted in such programmes than true resistance.

The largest influences of the type of forest regeneration on biotic risks are from: the quality and quantity of seedlings used in planting, the succession of silvicultural operations ending with artificial regeneration, and the vertical stand structure resulting from the regeneration process. In general it is apparent that artificial planting offers better conditions for pest and pathogen development than natural regeneration.

In intensively managed forests, cleaning and weed control have a positive effect on tree growth by decreasing competition for resources among the trees. However, although they may be beneficial for damage prevention (especially, by reducing forest fires and animal herbivores), their impact can also have negative impact on beneficial forest organisms, including the natural enemy fauna of many insect pests.

The change in the structure of the stand by thinning can have both positive and negative effects on forest vulnerability to biotic and abiotic hazards. Thinning can produce a cascade of possible effects, through the modification of the microclimate, changes in shape and vigor of remaining trees, and via the provision of food or shelters for beneficial or damaging organisms associated with dead wood and stumps. However, thinning probably has the largest effect on stand susceptibility to strong winds. It is difficult to assess overall changes in risk of disturbance following thinning, when taking the many different agents and different damage levels into account. Therefore, as there is no one thinning regime which lowers all the risks, an optimal regime must be adapted to the local conditions and risks.

Harvesting and tending are silvicultural operations that change ecological and physical characteristics in harvested and adjacent stands. These impacts relate to the method and intensity of harvesting and the time of logging at both yearly and forestry cycle scales. The impact of harvesting on damage by game, pest insects and fungal pathogens mainly results from the provision of food resources or accessible breeding material. Harvesting practices may also increase biotic risks of damage by mechanical injuries caused by the machinery.

The silvicultural operations that influence at most stand vulnerability to both biotic and abiotic hazards in European forests seem to be closely related to the species composition and the structure of the overstorey. Four main processes would drive the causal relationships between stand management and vulnerability: changes in individual tree physiology and development, effect on local microclimate, provision of fuel and resources to biotic and abiotic hazards, and enhancement of biological control by the natural enemies.

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Introduction

European forests are among the most intensively managed forests in the world. They are an important source of wood and non-wood products and provide numerous other services such as nature conservation, protection of soil and water, recreation possibilities and carbon storage. Despite their intensive use, forest resources are growing in Europe. The forest area is currently increasing by about 760 thousand ha (0.4%) per year (FAO, 2007) and the average growing stock has increased from 124 m³ ha⁻¹ in 1990 to 141 m³ ha⁻¹ in 2005 (FAO, 2007) and this is projected to continue for at least some decades to come (Schelhaas et al., 2006). However some other trends give reason for concern, particularly the increase in natural disturbances. Natural disturbances are any event such as fire, windstorms, ice, flood, pest or pathogen outbreaks that disrupt ecosystems' structure or function, generally for time periods longer than the current seasonal vegetation cycle. Because they often impair forest health and vitality, natural disturbances are highly relevant in the sustainable management of European forests (MCPFE, 2002). Schelhaas et al. (2003) estimated that the annual disturbed volume in the period 1950-2000 in total Europe equaled about 8.1% of the annual harvesting. However, in Central Europe this percentage was much higher, with an average value of 27% for Bayern in the period 1950-1995 (Mosandl and Felbermeier, 1999), 36% in the Czech Republic in the period 1956-1995 (Mosandl and Felbermeier, 1999) to 45% in Slovakia for the period 1985-1998 (Zubrik et al., 1999). According to the last FAO census (2007) about 10 million ha (6% of total forest area) were reported affected by natural disturbances in Europe over the 1998-2002 period. Many types of disturbances seem to be increasing over the past decades (Schelhaas et al., 2003), mainly in relation to changes in forest resource characteristics such as forest area, growing stock and share of conifers, but possibly also influenced by climate change.

Thus, evaluating the risk of disturbance events is crucial for forest management. Risks can theoretically be described by the surface of a triangle (Kron, 2002) where the sides reflect hazard, exposure and vulnerability. Any change in one of the sides of the triangle will lead to a corresponding change in risk level. Hazard is the probability of occurrence, which in forestry is usually related to the climate. Exposure can be interpreted as the values that are at stake, i.e. how well the forest fulfils its functions. Vulnerability (or susceptibility) relates to how easily a forest is damaged by the disturbance agent under consideration. Forest management can have a large influence on the vulnerability of the forest and can thus play an important role in reducing risks. For example the choice of the tree species to plant or regenerate, the preparation of the site, thinning or harvesting operations have profound effects on both the composition and structure of forests stands that may affect their susceptibility to biotic and abiotic hazards. The role of silviculture on forest

vulnerability to specific disturbance agents have been subject of many publications and textbooks before (e.g. Wainhouse 2005 for forest pest, Tainter and Baker 1996 for pathogens, Zajączkowski 1991 or Quine et al. 1995 for wind, Peterson et al. 2005 for fire). This approach is very useful in cases with high risk for a particular agent. However, a wide variety of disturbance agents exists, all with specific, sometimes contradictory characteristics relating to vulnerability as a function of stand management decisions. In order to decrease the risk of future disturbances impacting the functioning of the forest, we need a clear understanding on how management decisions influence the vulnerability for different agents at the same time. This would also contribute to fill the gap in practical knowledge on the side of the forest managers. Recently Blennow and Sallnäs (2002) in Southern Sweden showed that although forest owners rank storm highly as a potential risk, they generally do not know how to change their forest management to reduce the risk of damage.

The objective of this study is to synthesize available information of the effect of management options on vulnerability to different kinds of disturbance agents, at the forest stand level. Agents included in the overview are the most common biotic and abiotic hazards in Europe: mammal herbivores, pest insects, pathogenic fungi, wind and fire. We focus on European conditions, but literature outside Europe is included when relevant. We have divided the management operations into eight categories, according to a sequential order: site selection, site preparation, stand composition, tree genetic material, regeneration, thinning and pruning, cleaning and harvesting. For each of these management operations we review how they influence the vulnerability of the forest to the different disturbance agents and propose ecological explanations for these patterns. We focus on direct single effects because the scientific literature is too scarce to address the effects of combinations of management operations on forest vulnerability.

1. Site selection

Site selection plays a major role in the future vulnerability of newly established forest stands to disturbance. The occurrence and intensity of diverse biotic and abiotic hazards in forest habitats can commonly be associated with macro- and micro-climate, topographical features, or soil conditions. The local site conditions also affect the physiological state of the trees and thus their susceptibility to some biotic and abiotic damaging agents. Consequently, site-related predisposition to forest damage may be minimised by choosing sites less exposed to impairing factors and by matching given site conditions and the demands of the favoured tree species.

Patterns

The choice of habitat, and the associated potential forest damage by game, can to a certain extent be ascribed to topographic features. Red deer, *Cervus elaphus* and roe deer, *Capreolus capreolus* are generally attracted to localities which facilitate the acoustic, visual and olfactory control of the surrounding area. Hence, exposed sites such as ridges or plateaus are commonly visited, yet also valleys or basins offering food particularly for lactating females or protection against adverse weather conditions (Reimoser, 1986; Petrak, 1996).

Scientific literature provides a multitude of examples regarding the incidence of insect pests associated with certain site parameters. Mass attacks of the spruce bark beetle, *Ips typographus* in stands of Norway spruce, *Picea abies*, are frequently triggered by windthrow and often concentrate on south and west exposed sites and stand edges, even at higher elevations, above 1000 m a.s.l. (Wild, 1953; Worrell, 1983; Führer and Nopp, 2001; Baier et al., 2004; Wermelinger, 2004; Netherer & Nopp, 2005; Tykarski, 2006; Grodzki et al., 2006). Species composition shifts with the elevational gradient and mass propagation of some insect pests concentrate on certain altitudinal levels. Larch budmoth (*Zeiraphera diniana*) outbreaks are mainly observed at elevations between 1700m and 2000m in the Alps due to better temporal coincidence between tree bud-burst and insect egg hatching (Baltensweiler and Fischlin, 1988). While the little spruce sawfly, *Pristiphora abietina* meets optimal developmental conditions at elevations below 600 m a.s.l., Norway spruce stands at altitudes between 600 and 1200 m a.s.l are especially prone to infestation by the false spruce webworm, *Cephalcia abietis* and *Zeiraphera griseana* (Hb.) in the Sudeten (Capecki et al., 1989). Moreover, susceptibility of spruce stands to both sawfly species is positively correlated with soil moisture (Netherer & Führer, 1999; Führer & Nopp, 2001). Similarly, the lodgepole pine (*Pinus contorta*) is more susceptible to the defoliations of the pine beauty moth, *Panolis flammea*, in Scotland when planted on poorly drained sites (Hicks et al., 2001). Drought stress, on the other hand, predisposes seedlings of *Pinus sylvestris* to attacks of the large pine weevil, *Hylobius abietis* (Selander & Immonen, 1991), or can increase the susceptibility of *Picea sitchensis* to the green spruce aphid, *Elatobium abietinum* (Major, 1990). Drought stress also favours larval development of *Phoracantha* sp. (Hanks et al., 1999; Caldeira et al., 2002) in plantations of *Eucalyptus*. Mass outbreaks of *I. typographus* are frequently reported in context with sudden drought stress of Norway spruce stands not adapted to water deficiency, for stands stocking on xeric or shallow soils of high water permeability, or on soils with fluctuating water table and stagnic conditions, respectively (Merker and Müller, 1952; Wild, 1953; Worrell, 1983; Christiansen and Bakke, 1988; Wermelinger, 2004). Both, low and high soil productivity may predispose forest stands to insect attack. Pine stands on poorly drained or nutritionally deficient soils are prone to infestations by the

pine weevil, *Pissodes strobi* (Lavallée et al., 1996). Insufficient supply with basic cations and high soil and humus acidity enhances the predisposition of spruce stands to the sawflies *C. abietis* and *P. abietina* (Netherer and Führer, 1999; Führer and Nopp, 2001). On the other hand, forests of high productivity and the most vigorous trees within a stand are the most infected in the case of some lepidopteran species, such as the pine stem borer, *Dioryctria sylvestrella* (Carisey et al., 1994; Jactel et al., 1995). A positive response to increased nitrogen supply was found for *E. abietinum* and the grey pine aphid, *Schizolachnus pineti* (Kainulainen et al., 1996; Straw & Green, 2001) as well as for *P. abietina* (Schafellner et al., 1994, Schafellner et al., 1999), but not for the European pine sawfly, *Neodiprion sertifer* (Björkman et al., 1991). Nitrogen availability also seems to play a role in the vulnerability of *Pinus sylvestris* and *P. pinaster* seedlings to *H. abietis* (Selander and Immonen, 1992; Zas et al., 2006).

The probability of occurrence and potential intensity of fungal forest diseases depend in many respects on the locality of a given forest stand. Site criteria, such as water supply or soil temperature conditions may be crucial in the question whether forests are confronted with harmless saprophytic organisms or with pathogens. The parasitic status of the root disease, *Armillaria spp.* in stands of conifers is enhanced by either excess water supply or by drought stress of the host trees, as both conditions cause damage to the root system (Buckland, 1953; Manka, 1980; Wargo and Harrington, 1991). Root lesions, due to badly drained, compacted soils, periodic water deficiency or a particularly shallow soil water-table, also favour the infestation of spruce by the root rot, *Heterobasidion annosum* (Woodward et al., 1998). The pathogen benefits from either relatively high or low temperature conditions and an intermediate climate will reduce the incidence of decay. Sites above altitudes of 600m a.s.l. are known to be less prone to heavy infestation (Nopp, 1999; Thor et al., 2005). Korhonen et al. 1998 described the site factors that favour the occurrence of *H. annosum* as being: southernmost forests (south of 64°N), low altitude (below 600m), high soil pH and high lime content, high soil fertility and fluctuating water-table with some periods of drought, sites on former arable land or on former forest stands that were previously infected by *H. annosum*, and presence of neighbouring forests heavily infected by *H. annosum*. Temperature also plays a major role for the growth of the conifer root rot, *Rhizina undulata*, which meets optimum conditions for spore germination during forest fires (Baranyay, 1972). Sites that provide favourable conditions for spore infection, such as high humidity or low air movement, are particularly susceptible to fungal diseases. Hence, most severe damage caused by the pine shoot blight and canker, *Sphaeropsis sapinea* have been reported for protected valley sites (Wingfield and Swart, 1994). In turn, spruce stands on middle and upper, west-exposed slopes or hilltops, with high incidence of fog and westerly winds of high humidity are highly disposed to the shoot blight, *Sirococcus conigenus*

(Anglberger and Halmschlager, 2003). In a survey made in Spanish fir (*Abies alba*) forests, Solla and Camarero (2006) noticed that the number of trees affected by the rust fungus *Melampsorella caryophyllacearum* was significantly lower in stands at higher elevation, that had a southern aspect and were more distant from rivers. Frequently, the incidence of fungal infection is associated with certain soil conditions. In particular, increased severity of *S. sapinea* has been reported for sites fertilised by N:P:K (Blodgett et al. 2005) or for stands of *Pinus resinosa* and *P. nigra* prone to atmospheric deposition of nitrogen. Also outbreaks of Scleroderris canker, *Gremmeniella abietina* are associated with more fertile, nitrogen-rich soils. Environmental conditions favouring tree vitality also facilitated the infection of *P. pinaster* by the twisting rust fungus, *Melampsora pinitorqua* (Desprez-Lousteau and Wagner, 1997a). However, sites with nutrient poor soils are not necessarily less predisposed to fungi. High susceptibility of Norway spruce to *S. conigenus* and *Armillaria spp.* is associated with soil degradation, low pH values and deficiency of basic cations (Singh, 1983; Nopp, 1999; Jandl et al., 2000). Nutrient deficiency also enhances the risk of infection by *H. annosum*, which is, however, in the same time favoured by high pH values of the soil and increased contents of Ca (Piri, 1998; Nopp, 1999; Thor et al., 2005b). Vollbrecht and Agestam (1995) observed root rot to cause particular high damage in stands established on former agricultural land, used as fields or for grazing.

A range of site factors influence the chance and possible dimension of windthrow in forest stands. Overall, the occurrence of strong winds increases with elevation (Winterhoff et al., 1995; Ni Dhubhain et al., 2001). Depending on the prevailing wind direction, slopes of certain gradients and exposure are especially prone to storm damage (Werner and Armann, 1955; Schreiner et al., 1996; Ni Dhubhain et al., 2001, Quine et al., 1995). Steep slopes tend to have shallow soils, and the development of roots, associated anchorage and windthrow risk, may be altered by the slope (Nicoll et al. 2005). Any factor that decreases rooting depth can negatively affect anchorage (Coutts et al., 1999), such as frequent waterlogging (Van Nispen tot Sevenaer, 1975; Laiho, 1987; Offergeld, 1986; Poeppel, 1994; Ray and Nicoll, 1998; Schreiner et al., 1996) or soil compaction (Andersen, 1954). The effect of such adverse conditions on stand stability varies with the tree species (Nicoll et al., 2006), as well as the rooting system's ability to adapt to wind stress on the tree (Nicoll and Ray, 1996; Xu et al., 1997;). Attempts to overcome such limitations by site preparation are successful in some cases (Ray and Nicoll, 1998), however even where rooting depth is improved by site cultivation, the cultivation method itself (for example with ploughing to lower a water-table) can reduce anchorage by reducing lateral spread of structural roots. In addition, where root anchorage is improved, there is a risk that the predominant form of damage becomes wind breakage instead of uprooting, leading to even higher wood losses (Studholme, 1995). Previous land use is also relevant

to forest stability, because of the enhanced susceptibility of conifer stands on former arable land to *Heterobasidion* root rot (Soest, 1954).

Several studies have shown that the risk of fire is also affected by aspect, slope and altitude. Forests stocking on xeric sites of high solar irradiation are highly predisposed to burning (e.g. Mouillot et al. 2003; Mermoz et al. 2005; Gonzalez and Pukkala 2007). The incidence and spreading rate of fire usually increases with the steepness of slopes (e.g. Agee, 1993; Vasquez and Moreno, 2001; Diaz-Delgado et al., 2004) where there is an increasing radiant energy transfer from flaming fronts to upslope fuels (Rothermel and Philpot, 1983; Pyne et al., 1996). The effect of altitude depends on the specific location. For example, while studies in central Spain (Vasquez and Moreno 1995) and Catalonia (Diaz-Delgado et al. 2004; Gonzalez et al. 2006; Gonzalez and Pukkala 2007) showed a greater risk of burning in areas below 800-1000 m elevation compared to areas of higher altitude, Mermoz et al. (2005) showed a greater fire risk at intermediate elevations (900-1100 m) in the mountains of northern Patagonia.

Explanations

When comparing the patterns of forest disturbance with respect to site related parameters, some analogies become evident. There are specific environmental preconditions which influence even very different factors in a similar way and especially predispose forests to damage.

A striking example for such general causality is the effectiveness of temperature. Thermal conditions play a crucial role in the success of many organisms, influencing growth, population dynamics, and survival. Relatively warm, protected sites serve as habitat for a variety of species, being preferred to localities exposed to harsher climate. For instance, red deer tend to visit valleys and lower slopes during late wintertime, where the ungulates find protection against rough weather and a better supply of food due to the higher ambient temperatures and the earlier start of the season (Führer & Nopp 2001). Many insect species meet their optimum conditions for reproduction and development within a certain temperature range, which is offered by “warm” forest sites. Mass outbreaks of forest pests are commonly associated with high temperatures or precipitation deficits. For example, increased temperature during the hibernation of bark beetles followed by a long vegetation period promotes an early emergence of the beetles in spring and the establishment of several generations during the year. In temperate forests, the optimal temperature for mycelium growth of most pathogenic fungi is between 20 and 30°C (Tainter and Baker, 1996). Higher temperatures benefit the development of forest pathogens that have been introduced from

Mediterranean or tropical countries, such as *Sphaeropsis sapinea*, *Phytophthora* spp. and *Biscogniauxia mediterranea* (Desprez-Loustau et al 2006). The intensity of *Scleroderris* canker damage on lodgepole pine increases in Sweden with both altitude and latitude due to a preference for lower temperatures (Karlman et al., 1994), whereas damage by *Phytophthora cinnamomi* on red oak is restricted to the south-western part of France due to the sensitivity of the pathogen to cold temperatures in winter (Marçais et al., 2004).

At the same time, the vitality of the host trees may be impaired due to drought stress. A susceptibility rating system developed by Shore & Safranyik (1999) is based on these interrelations and includes latitude and longitude as well as elevation, largely to reflect the impact of temperature on survival of the mountain pine beetle, *Dendroctonus ponderosae*. The disease *Fusarium circinatum* is observed to be progressing significantly faster in the coastal zone of California than in more inland locations, largely as a consequence of a requirement of the pathogen for humid weather conditions (Wikler et al., 2003). Macroclimatic conditions are modified by site related features such as elevation, aspect and topography, which also, to a certain extent, reflect water and nutrient supply of forest stands. Slopes exposed to high rates of solar irradiation or stands on upper slopes, ridges or hilltops are particularly prone to damage caused by water or nutrient deficiency, and storm. The risk of fire in a forest stand increases with temperature and drought. Such precedent damage may enhance vulnerability of stands to infestation by insect pests or fungal diseases. In this way, elevated temperature conditions, combined with high humidity and damage to the root systems, promotes more effective infection by a range of fungal species.

Forest health is strongly dependant on soil conditions and the adaptation of plants to given states of soil structure, moisture, acidity or nutrient availability. Soil moisture deficits resulting in moisture stress of the host plants can in many cases be correlated with elevated insect or fungal damage (Stone 2001, Desprez-Loustau et al 2006). Again, bark beetles may serve as a good example, preferentially attacking drought stressed trees. Humidity plays an important role in the mortality of insects pupating in the upper soil or humus layers, such as certain species of sawflies or moths. For example, increased mortality rates among pro-nymphs and pupae of *P. abietina* are due to oxygen deficiency and infestation by fungi favoured by high soil moisture (Netherer and Führer ,1999; Führer and Nopp, 2001). Survival of pupating sawflies, on the other hand, is enhanced by the insufficient supply of soils with basic cations and high soil acidity, parameters that may strongly impair tree vitality. Soil water content is an important factor for the development of root rot fungi. In oak forests, the pathogenicity of *Collybia fusipes* is reduced in hydromorphic soils due to a lack of oxygen (Camy et al., 2003). The spread of *Phytophthora*'s infectious propagules, which are free-

moving in water, is favored by soil humidity and particularly by irrigation in tree nurseries (Husson et al., 2006). Adverse conditions in the rhizosphere leading to lesions of the root system render forest stands especially vulnerable to fungal diseases and windthrow. The reason why the reverse is not true, i.e. that forest health has not been related to high soil productivity, may be explained by the enhanced nutritional quality of well supplied stands for diverse pests and pathogens. As an example, the high susceptibility of *Pinus pinaster* stands to the pine moths *D. sylvestrella* may be due to the thickness and nutritional quality of the phloem (Carisey et al., 1994; Jactel et al., 1995). Many studies of fungal disease also point to a positive relationship between soil fertility and risk of infection. There is considerable evidence that the enhanced availability of nitrogen is a key factor in the improved nutritional quality of host tree foliage to not all, but various forest pests (Kyto et al., 1996a,b; Pinkard et al., 2006). Hence, forest sites affected by nitrogen input, either originating from fertilised, adjacent agricultural land or from atmospheric deposition of pollutants, may be especially prone to herbivory. Elevated supply of nitrogen may cause water stress or a reduction of fungistatic phenolic compounds in the roots of the host trees and thus decrease tree vigour (De Kam et al., 1991; Stanosz and Trobaugh, 1996; Tomova et al., 2005).

However, the regional incidence of damage may remain low where the necessary preconditions do not occur. Regarding biotic agents, the suitability of sites as habitats and the availability of food play a particularly important role. This interrelation is well demonstrated by the predisposition of some forests to bark stripping of red deer during wintertime. The probability of damage is both influenced by the accessibility and the food supply of areas frequented by red deer. Steep slopes without snow cover, offering security due to the absence of people and increased sight distances are highly attractive, but may still be less damaged because of insufficient available food. On the other hand, forests that are less intensely frequented may suffer greatly from stem injuries, when high snow cover forces red deer to switch to bark stripping instead of feeding on the forest floor (Schwerdtfeger, 1981; Georgii and Schröder, 1983; Führer and Nopp, 2001). Insect pests benefit, in many cases, from a surplus of food and breeding opportunities, e.g. due to the uniformity of forest stands or foregoing catastrophic events. For instance, lowland stands of Norway spruce in Austria are highly prone both to mass outbreaks of the little spruce sawfly, *P. abietina*, and the bark beetles *I. typographus* and *Pityogenes chalcographus*. The favourable climatic conditions of the lowlands provide the former with optimum conditions for egg deposition, coinciding with the optimal shoot state of spruce and the latter find highly susceptible trees for infestation. Bark beetle epidemics are in general favoured by frequent abiotic disturbances, such as windthrow, snow breakage, or fire, providing excess food supplies. Figuratively, the abiotic agent fire also depends on the availability of “food”, whereby altitude and aspect determine fuel supply and moisture of forest stands. Besides

the variations in climate, altitudinal patterns in stand vulnerability result from the probability of ignitions through human activities, as altitude is usually negatively correlated with population density.

Conclusion

The correlation of certain risks with typical site characteristics of forest stands can be ascribed to the presence of specific preconditions favouring the occurrence of given biotic or abiotic agents and promoting the tree susceptibility to these hazards. The pathogenicity of organisms possibly harmful to forests may vary with the attractiveness of localities as habitat, with climatic conditions influencing their development, with the availability and quality of food, and with the status of tree physiology. Regarding abiotic forces, the probability of detriment depends on the general exposure of sites to the agent (e.g. frequency of storms, fire ignition patterns), climatic conditions modifying its power (e.g. more fire events in case of high temperature, drought and winds) and the susceptibility of affected forests to the hazard (e.g. wood moisture and combustibility).

2. Site preparation

In many cases forest management has to cope with given site characteristics, either because of lacking alternatives or the will to subordinate management goals to environmental conditions. Consequently, techniques of site preparation which improve the conditions for afforestation or regeneration and growth are especially common in intensive forestry, comprising water management, such as drainage and irrigation, soil cultivation by ploughing, harrowing, scarification or mounding. These silvicultural treatments, as well as decisions concerning brash and stump management, weed control, prescribed burning, fertilisation, and the use of fallow periods may affect forest health in either positive or negative ways, depending on the type of application and the hazard.

Patterns

As foresters are often required to avoid fencing of regeneration areas for economic or environmental reasons, many studies have been conducted to identify practices that might reduce damage from mammal herbivores. Studies conducted in Scandinavian countries showed that weed control can reduce browsing by roe and red deer (Huss and Olberg, 1982; Roth and Newton, 1996)

as well as by voles (*Clethrionomys* spp. and *Microtus* spp.). In contrast, the removal of woody debris after a clear-cut has almost no impact on browsing (Bergquist and Orlander, 1998b). However brush management may reduce refuges for small rodents that feed on newly planted seedlings and can cause significant damage (Wingfield and Swart, 1994). In some cases, prescribed burning can be used to limit the incidence of these rodents (Savill et al., 1997). Some practices like mounding may also increase browsing by roe deer (*Capreolus capreolus*) (Bergquist et al. 2001). Nitrogen fertilization is known to increase the palatability of birch seedlings to voles (Rousi et al., 1993) and to hares (Mattson et al., 2004). Bergquist et al. (2001) found no significant difference in roe deer browsing damage on Norway spruce seedlings planted in scarified and control clearcuts.

The adult pine weevils *Hylobius abietis* cause most damage by feeding on the bark of young seedlings after their emergence from stumps where they developed as larvae. The post-harvesting removal of stumps and roots has therefore been proposed to reduce *H. abietis* damage in conifer afforestations but it remains difficult to apply (Speight and Wainhouse, 1989). Of more practical interest is to postpone the planting after the clear-cut and a fallow period of one to three years has proved to significantly decrease pine weevils damage on young conifers (Doom and Franken, 1980; von Sydow, 1997). More generally brush and slash removal before planting may reduce breeding substrate for some insects and then limit the damage. Several small bark beetle species like *Ips pini* (Gara et al., 1999; Six et al., 2002), *Hylastes angustatus* (Wingfield and Swart, 1994) or *Pityogenes chalcographus* can build up their population on woody debris and then attack living trees. Larger scolytid species like *Ips typographus*, even though they do not develop on small woody debris, may be attracted by the bark odours released from residual wood and then attack living trees in the vicinity (Vaupel et al., 1981). This is discussed further in the *thinning* section.

Scarification, which consists of vegetation removal to expose underlying soil, is the most common action to facilitate regeneration. Scarification significantly reduces pine weevil (*Hylobus abietis*) damage and increases seedling survival in Norway spruce (Petersson et al., 2006; Orlander and Norlander, 2003; von Sydow, 1997) and Scots pine (Pitkanen et al., 2005). Mounding (removal of a patch of surface soil) also significantly decreases pine weevil damage on planted Norway spruce (Heiskanen and Viiri, 2005). However the rate of feeding damage to Scots pine seedlings caused by pine weevils (*Hylobius abietis* and *Hylobius pinastri*) has been showed to be higher on prescribed burned clearcut sites than on unburned ones (Pitkanen et al., 2005). In some tree defoliators like the pine sawflies *Acantholyda* and the pine processionary moth *Thaumetopoea pityocampa*, late larvae move to warm and sunny areas to dig into the soil and pupate and they may benefit from scarified sites to burrow and thereby improve their survival rate.

There is a widely held belief that fertilization can enhance forest resistance to insect pests by improving tree growth and vigour. However, recent studies suggest that fertilization is more likely to decrease tree resistance to insect pests (Wainhouse, 2005). For example the damage by the pine weevil *Hylobius abietis* was greater in fertilized maritime pine (*Pinus pinaster*) plants than in the unfertilized control trees (Zas et al., 2006). The stem borer *Dioryctria sylvestrella* showed higher damage in maritime pines fertilized with phosphorus (Jactel et al., 1996). The spruce sawfly *Gilpinia hercyniae* and the green spruce aphid *Elatobium abietinum* also performed better in nitrogen fertilised Sitka spruce (Wainhouse et al., 1998). In addition, some studies have demonstrated negative effects of fertilization on the abundance or survival of some forest insects (see Speight and Wainhouse, 1989 and references herein). For example chewers like the pine sawflies *Neodiprion swaneii* and *Neodiprion sertifer* were adversely affected by nitrogen fertilization of jack pine and Scots pine respectively (Smirnoff and Bernier, 1973; Larsson and Tenow, 1984). Fertilization also resulted in a reduction of leaf roller (*Byctiscus populi*) and chrysomelid damage (*Chrysomela tremulae* and *Phratora vitellinae*) in poplars (Gruppe et al., 1999). However Carrow and Betts (1973) observed both positive and negative effects of nitrogen fertilization on the aphid *Adelges piceae* in the grand fir *Abies grandis*. Nitrogen fertilization increased infestation levels of the pine shoot moth *Rhyacionia frustrana* in loblolly pine (*Pinus taeda*) whereas phosphorus applications tended to decrease infestation rate (Sun et al., 2000).

The infection by the root rot *Heterobasidion annosum* starts when fungal spores land on fresh cut stump surfaces. The fungus grows through the remaining root system into nearby live trees via root grafts or contacts. The removal of stumps before planting is therefore a management practice that can reduce *H. annosum* damage (Korhonen et al., 1998; Gibbs et al., 2002). It is also the most effective way to reduce the inoculum pressure from *Armillaria* (Legrand et al., 2005). Because older stumps are less suitable to the development of spores, a fallow period between clear cutting and reforestation has been successfully applied to reduce its impact on Corsican pine in England (Gibbs et al., 2002). Scarification can also contribute to minimize infection risk by root rot (van Halder et al., 2002). Slash burning generally reduces the inoculum potential of *H. annosum* (Korhonen et al., 1998) but not of *Armillaria* (Legrand et al., 2005). Slash removal prevents the expansion of the charcoal disease (*Biscogniauxia mediterranea*) in cork oak (*Quercus suber*) and of the *Botryosphaeria dothidea* canker in Eucalypt forest (van Halder et al., 2002). In contrast ploughing may increase the damage of root rot fungi like *H. annosum* (Redfern, 1984) and *Armillaria ostoyae* (Lung et al., 1997) in pine plantation via the dissemination of rhizomorphs, the quiescent form of the fungi in the soil (van Halder et al., 2002). Likewise prescribed burning may

enhance some root rot diseases such as *Rhizina inflata* (Savill et al., 1997) and *R. undilata* (Germishuizen, 1984) but can be used to limit the development of the brown spot needle blight (*Mycosphaerella dearnessii*) a foliar disease of pines which persists in infected needle litter on the ground (van Halder et al., 2002).

Fertilisation may also have either positive or negative effects on forest pathogens. Damage by *Hypoxylon mediterraneum* is reduced in fertilised oak stands and fertilised poplar stands suffer less from secondary diseases which tend to develop on stressed trees (Lanier et al., 1994). Fertilisation with nitrogen led to delayed and decreased colonisation of spruce needles by the fungal endophyte, *Lophodermium piceae* (Lehtijarvi and Barklund, 1999). On the other hand, fertilization before plantation is also known to slightly predispose pine trees to the *Cronartium* fusiform rust infection (Miller, 1977; Burns et al., 1980; Powers et al., 1981; Hodd et al., 1988; Shoulders et al., 1990; Schmidt et al., 1995). Nitrogen fertilisation has been shown to promote infection by *Mycosphaerella pini*, *Mycosphaerella quercina*, *Cryptodiaporthe populea* and *Melampsora pinitorqua* (Lopez-Upton et al., 2000) and phosphorus fertilisation can increase damage by pine twisting rust, *M. pinitorqua* (Desprez-Loustau and Wagner, 1997b). No clear effect of fertilisation has been observed on *Armillaria* (Legrand et al., 2005) and *H. annosum* (Korhonen et al., 1998) occurrence or damage.

Site preparation can be used to improve rooting conditions and thus to increase stability to wind. Drainage and tilling can increase the effective rooting depth (Ray and Nicoll, 1998; Ni Dhubhain et al., 2001), but preparation and planting methods should ensure the development of a symmetric root system (Coutts et al., 1999). Hendrick (1986) notes that, in Ireland much planting has been done along open furrows, which encourages the root system to develop only on one side, causing instability. However, Studholme (1995) describes a deliberate no-till strategy in a particularly windy area to avoid a replacement of uprooting by stem breakage. The nitrogen fertilization which favours the development of branches and leaves may also reduce the bending resistance of trees (Mitchell, 2003).

Whenever site preparation involves shrub clearing or increased moisture content, this will significantly decrease fire hazard, as both fuel load and moisture are key aspects influencing fire ignition, spread and intensity (Rothermel and Philpot, 1983) (see comments under section “Weeding, shrub removal and prescribed burning”). Conversely, when fertilization results in faster understorey growth, it may increase fire risk. Prescribed burning may improve the recruitment of tree seedlings in natural regenerations. Some Mediterranean pines, such as *Pinus halepensis* are

considered pioneer species whose recovery strategy relies on rapid seedling recruitment after fire (Abbas et al., 1984).

Explanations

It appears that most positive effects on forest health of stump, brash or understorey removal during site preparation can be attributed to a reduction in the amount of resources for biotic and abiotic damaging agents. Basically, stumps represent the breeding substrate of *Hylobius abietis* and *Heterobasidion annosum*, which are among the most severe pests and pathogens in European conifer forests, and destruction of the substrate will decrease the risk of infection to neighbouring living trees. The use of a fallow period between final harvesting and reforestation is just another way to reduce the quality of the breeding substrate, taking advantage of progressive decomposition of the stumps. Similarly some bark beetles find breeding resources in woody debris, and slash management prevents them from building up their population to the high levels that would lead them to attack living trees. The mechanism with fire is not dissimilar as shrubs and dead branches lying on the ground represent a fuel resource that may maintain a forest fire and increase the threat to canopy trees. By analogy one could suggest that site preparation operations which provide better resources for the growth of tree roots will in turn increase stand resistance to strong winds. Even though they do not directly feed on these substrates, some biotic damaging agents can find shelter in the forest understorey or in harvesting residues, and this would explain why scarification can have negative effects on their abundance. It has been hypothesised that weeds or dead branches provide pine weevils with a protection against predators or adverse climatic conditions (Björklund et al., 2003). Likewise, the number of roe deer visits increases with the age of clearcuts, probably due to the increasing amount of available food in the early vegetation succession (Gill et al., 1996; Bergquist and Orlander, 1998a) but also due to the shelter provided by a high understorey which promotes a feeling of safety (Petersson and Orlander 2003). Conversely, scarification may benefit some insect defoliators, such as pine sawflies and the pine processionary moth, because bare soil areas represent optimal conditions for larvae to bury and pupate, thereby increasing the survival rate of the population (Markalas 1989).

The effects of fertilisation on forest health is somehow more difficult to interpret as the results of experiments appear contradictory, with both positive and negative effects, sometimes on the same pest or where the use of different fertiliser, such as N or P, may lead to opposite effects. However beside these apparent contradictions, causal relationships between fertilisation and tree resistance have recently been demonstrated (e.g. Kyto et al., 1996 a,b), which are elegantly summarized by

Wainhouse (2005). The first obvious effect of fertilisation is that it can improve the quality of food for some insect pests and pathogenic fungi. In particular, the use of nitrogen fertilisers results in increased leaf N content which will benefit leaf chewers, including some sawflies and moths, phloem feeders such as aphids and scale insects, and some gall makers. This explains the contradictory results observed with N and P fertilization depending on the nutrient requirement by the pest and pathogen species. For the same reasons several foliar diseases, particularly some rusts, would also benefit from this higher N content. Furthermore, phosphorus fertilisation induced changes in the nutritional status of pines which were then more damaged by the twisting rust (Desprez-Loustau and Wagner, 1997b). According to the growth – differentiation balance hypothesis (GDBH) (Herms and Mattson, 1992) less carbon is allocated to carbon-based secondary chemicals when growth is enhanced by fertilisation. Fertilised trees, with lower concentration of secondary chemicals which are toxic for many pest insects and fungal pathogens, would then be less able to defend themselves. However, fertilization of extremely nutrient-limited plants is predicted to increase secondary metabolism if photosynthesis is also increased (Herms, 2002) which would explain the negative effects of fertilization on some pests and pathogens in particular cases. Moreover a fertilization-induced biomass increase may provide the plant with better tolerance to defoliation. It has been observed that the number and size of resin ducts increase in fertilised conifers (Kyto, 1999; Wainhouse et al., 2005). Because resin compounds are toxic for bark feeders such as bark beetle and weevils (Wainhouse et al., 2005) or repellent for mammal herbivores such as voles and hares (Harju et Tahvanainen, 1997), it follows that fertilised trees would be less damaged by these bio-aggressors.

Conclusion

It seems that the change in biotic risk in response to forest fertilisation depends on the type and amount of fertilizer, on the feeding regime of the pests and pathogens and on the balance between the fertilization-induced changes in food quality and secondary metabolite concentrations. It is therefore difficult to derive any general recommendation on the use of fertilisers, besides that fertilisation is probably of limited value to manage health problems in forests (Wainhouse, 2005). More relevant is probably the management of harvesting residues and understorey vegetation to deprive both biotic and abiotic agents of the fuel, resources and shelter that they might use to build up their population or increase their strength. However such practices may lead to negative effects on biodiversity as dead woody debris and understorey plants provide habitats for the majority of forest dwelling species.

3. Stand composition

The primary decision to make before afforesting or reforesting is to select the tree species. This may depend on site conditions and on market or public demand for forest products or services, but once the decision is made it will influence most of the silvicultural practices to be implemented. Forest owners or managers will then have to decide if this tree species will be grown alone or in association with other species, i.e. if they will implement pure or mixed stand forestry. The rationale behind growing mixed forests is the traditional wisdom that it is risky to put all one's eggs in one basket. As far back as 1828, the German silviculturist von Cotta nicely summed this up by saying that "since not all tree species utilize resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also a wider range of timber will be available to satisfy different demands..." (translated by Scherer-Lorenzen et al., 2005). In the recent decades, with increasing awareness of the accelerating loss of earth's species (Balmford and Bond, 2005), a considerable research effort have been made toward a better understanding of the role of biodiversity in ecosystem functioning (Hooper et al., 2005). Recently Scherer-Lorenzen et al., (2005) showed that forest diversity can have various effects on ecosystem processes and stability against disturbances. However no consistent response of forest functioning to tree diversity changes was reported as the effects of biodiversity may vary with the composition of tree species assemblages, the type of ecosystem function and its interaction with the abiotic environment (including management).

Patterns

In a meta-analysis of the scientific literature, Jactel and Brockerhoff (2007) gathered 119 individual studies where the mean damage from a pest insect species on a particular tree species was compared in pure vs. mixed stands in the same area and time period. This analysis, involving 33 insect taxa and 33 tree species, revealed that in almost 80% of the cases tree species grown in pure stands are significantly more damaged by herbivorous insects than in more diverse stands. However this outcome varied with the host specificity of pest insects. Herbivory by oligophagous insect, feeding within a genus or a family of tree species was almost always reduced in mixed stands (93% of the cases). For example the scale insect *Matsucoccus feytaudi*, which is highly specific to the maritime pine (*Pinus pinaster*), showed significantly higher infestations in pure stands of maritime pine than in mixed stands with the Corsican pine (*Pinus nigra laricio*) (Jactel et al., 2006). The pine processionary moth, *Thaumetopea pityocampa*, mainly feeding on *Pinus* and *Cedrus*, made lower defoliation in the Corsican pine when mixed with the common beech *Fagus sylvatica* (Géri, 1980). The gall mite *Acalitus rudis*, specialised on birch species, made significantly more damage in

monocultures of *Betula pendula* than in mixtures with Scots pine (Vehviläinen et al., 2006b). In contrast, the effect of tree diversity on polyphagous pest insects, feeding on several tree families, was more variable with a reduction of damage in mixed stands in only 60% of the cases. The large pine weevil *Hylobius abietis* is a serious pest of conifers in Europe, feeding on pines, spruces and firs. It can also make damage on a large array of deciduous trees such as alder, birch, ash, beech, oak, cherry and lime (Löf et al. 2003). Damages by *H. abietis* on spruce seedlings are consistently higher in pure stands than in mixed stands with a shelter of pine species (von Sydow and Örlander, 1994; Örlander et al., 2001; Nordlander et al., 2003; Peterson and Örlander, 2003). *Lymantria dispar*, the Gypsy moth, is one of the most polyphagous pest insect, feeding on hundred of deciduous or coniferous trees. In the United States, where *L. dispar* causes considerable damage after its introduction, and contrary to the overall pattern of lower herbivory in mixed forests, pines are less damaged by the Gypsy moth in pure stands than in mixtures with oaks (Brown et al., 1988; Gottschalk and Twery, 1989).

The studies that addressed the effect of forest stand diversity on herbivory by mammalian grazers are much fewer and they are mainly restricted to damage on pine seedlings in boreal forests. In experimental tests, where young cut trees were driven into the soil to mimic forest stand, no significant difference in moose (*Alces alces*) damage on Scots pine seedlings were observed between pure stands or mixed stands with alder or aspen trees (Danell et al., 1991; Edenius, 1991). In two other studies made in young plantations, moose browsing was higher in mixed stands than in pure stands of Scots pine, particularly when other, more preferred host trees like birch (Vehviläinen and Koricheva, 2006a), aspen, rowan or willow (Heikkilä and Härkönen, 1996) were present. The level of bark stripping by the red deer *Cervus elaphus* was not correlated to the number of tree species in forest stands (Verheyden et al., 2006). However, in any case, damage by this large polyphagous grazer was reduced in mixed stands. In contrast, with smaller, more specialised mammalian herbivores such as voles and hares, some mixtures experienced lower grazing than pure stands, notably when more palatable tree or plant species were available (Hjälten et al., 1993, Vehviläinen and Koricheva, 2006). These outcomes are therefore consistent with those obtained from pest insect studies showing that damage in tree mixture depends on both the feeding specialisation of herbivores and the composition of mixed stands in more or less preferred host tree species.

Two recent review articles dealt with forest stand diversity effects on susceptibility to fungal pathogens in boreal and temperate forests (Pautasso et al., 2005; Koricheva et al., 2006). They report on reduced damage or slower spread in mixed stands for several fungal diseases such as the

Armillaria root rot (Morrison et al., 1988; Greig et al., 2001; Gerlach et al., 1997), the *Ceratocystis fagacearum* oak wilt (Menges and Loucks, 1984), and the *Gremmeniella abietina* lodgepole pine canker (Karlman et al., 1994). However the best documented case concerns the *Heterobasidion annosum* root rot. Korhonen et al (1998) reviewed thirteen studies in which the incidence of the butt rot was compared in mixed vs. pure stands of pine, spruce or fir. In nine studies lower abundance or damage of *H. annosum* was observed in mixed stands. Later Thor and Stenlid (2005) showed that the root rot incidence on Norway spruce (*Picea abies*) was negatively correlated with the proportion of spruce in the stand. Almost 70% of the cases therefore support the view that the admixture of other species would decrease the probability of *H. annosum* damage in conifer stands, whereas 20% of the studies showed no significant differences between pure and mixed stands and 10% higher incidence in mixed stands. McCauley and Cook (1980) found a similar relationship with the proportion of Douglas fir in forest stands, the preferred host, which positively related with the abundance of the *Phellinus weirii* root rot in North America. Tree species diversity may not reduce susceptibility to more generalist pathogens. One of the most generalist and aggressive root pathogen is indisputably *Phytophthora cinnamomi*. Once introduced in Australia, and despite their high tree and shrub species diversity, native eucalypt forests were highly susceptible to this fungal pathogen (McDougall et al. 2002). Finally associating particular tree species may increase mixed stand vulnerability to the heteroecious fungal pathogens. These fungi require two alternate, unrelated hosts to complete their life cycle and if these host trees are present in the same mixture the latter are more likely to experience more severe damage. The best known example is the pine twisting rust caused by *Melampsora pinitorqua* which uses Scots pine and aspen (*Populus tremula*) as main hosts. As expected, the susceptibility of pine stands increases with the abundance of aspens in the stands (Mattila, 2002, 2005). Recently, *Phytophthora ramorum* and *kernoviae* have been found infecting oak and beech in England with rhododendron and viburnum serving as reservoir hosts (Brasier et al., 2005).

Stand composition undoubtedly plays a role in susceptibility to wind damage, but the literature on the subject does not always agree. Several authors report a higher stability of mixed species stands as compared to monocultures (Werner and Armann, 1955; Henkel, 1960; Slodicak, 1995; Lokes and Dandul, 2000; Schütz et al., 2006). However, others argue that damage to a mixed species stand will only be reduced equal to the share of the stable species (Lüpke and Spellmann, 1997), or that the combination could become even more unstable (Savill, 1983). In a recent review Dhôte (2005) concluded that tree species identity is more important to predict wind damage than the difference between pure and mixed stands and that the stability to strong winds of sensitive species is not improved when mixed with more stable species. However he pointed out that mixing species would

result in less massive damage but in more single tree windthrow so that mixed stands are in better position to regenerate. Schelhaas (2007) concluded in a modelling study that mixture effects were likely to depend on stand treatment and history.

The presence and abundance of different forest species have been mentioned as an important factor driving the behaviour of fire. Different species present different characteristics in terms of morphology, shade tolerance, moisture content, and chemical composition that influence the availability and combustibility of the forest fuels (Dimitrakopoulos and Papaioannou, 2001; Wang, 2002). For example, coniferous species have been pointed out as high flammable due to the high content of resins and essential oils (Velez, 1990 Bond and Van Wilgen, 1996; Dimitrakopoulos and Papaioannou, 2001), increasing not only the probability of fire occurrence in pine dominated forest (González et al., 2006; Moreira et al., 2001) but also the potential damage caused by fire in terms of fire severity and tree mortality (Wang 2002; González et al 2007b). Thus, the fire hazard of pure conifer stands is usually higher than the one of deciduous hardwoods, whereas mixed conifer-deciduous stands have intermediate fire hazard (Moreira et al. 2001, González et al 2006). However stand composition is often linked to climatic features (e.g. deciduous broadleaves occur in moist sites in the Mediterranean region), microclimatic conditions (inside the forest stand) or vertical vegetation structure (stand structure) that may confound the isolated effect of species composition. A recent study by Fernandes and Rigolot (2007) suggests that stand structure is more important than stand composition in determining potential fire behaviour in Portuguese forests.

Explanations

At the forest level the maintenance of high tree diversity has the obvious advantage of spreading the risk. Because not all of the trees are susceptible to all biotic or abiotic hazards, the more tree species in a stand the more likely is this stand to accommodate trees that will escape infection, infestation, breakage or fire damage. These spared trees may then fill the gaps, maintaining the structure and the functioning of the forest. A major argument for mixed stand forestry is the 'insurance hypothesis' (Loreau et al., 2001; Pautasso et al., 2005), not so far from the "eggs in a basket" story, which states that more diverse ecosystems will respond in a more buffered way to disturbance (higher resistance) and recover more quickly (higher resilience) than monocultures. This is well illustrated by the capacity of forests to recover after fire. Tree survival is dependent not only on the intensity of the fire but also on the protective mechanisms developed by the tree, as bark thickness or the capability of resprouting. For example, some hardwood species like *Quercus coccifera*, *Q ilex* and *Q suber*, may present a high resprouting capability which allows them to increase their probability to

survive forest fires (Trabaud, 1987; Retana et al., 1992; Pausas 1997, 1999), a characteristic quite rare in coniferous species. Mixed stands with such broadleaved species will then have a better chance of regeneration than pure conifer stands.

When considering a particular tree species, two main ecological hypotheses can be advanced to explain why it may or may be not grown in mixed stands to reduce the risk of biotic damage: the accessibility of host trees and the impact of natural enemies. The admixture of other species with a focus tree species, a wood productive species for example, is expected to raise several barriers that may reduce its accessibility and then its use by grazers, insect pests or fungal pathogens (Jactel et al., 2005). The first barrier is quantitative as for a given stand surface increasing the number of tree species will decrease the abundance of trees from the focus species. The lower concentration of food resources may in turn prevent pest and pathogens from developing and building up their populations thus reducing the risk of damage on focus trees. Second, non-host trees may provide physical or chemical barriers to host location or colonization. Some insect species, such as the spruce budworm *Choristoneura fumiferana*, are wind dispersed as larvae, just as many fungal pathogens are wind dispersed by aerial spores. The more diverse a stand the lower the chance that these passively dispersed propagules land on the right host tree thus limiting the risk of establishment (Kemp and Simmons, 1979; Heybroek, 1982). Several tree diseases, such as root rots, spread through root contacts or root grafts. The presence of non-host trees in between two neighbouring focus trees may then prevent pathogens (such as *H. annosum*) from reaching new host trees, (Linden and Vollbrecht, 2002). For those forest insects (Watt, 1992) and mammalian herbivores (Pietrzykowski et al., 2003) which use visual cues to locate their host, mixing different tree species will result in hiding host trees. Chemical stimuli can also determine the risk of herbivory by insects and mammals. For example, conifer-inhabiting bark beetles are able to perceive non-host volatiles released by angiosperm trees and to use them to avoid non suitable habitats. Because mixed forests have greater semiochemical diversity than pure forests they would reduce the likelihood of bark beetles outbreaks (Zhang and Schlyter, 2004). In mixed stands host tree saplings can also be protected against large herbivores such as mammalian grazers by non-host, nurse plants in the form of physically (thorns) or chemically (toxins) defensive species (Smit et al., 2007). These hypotheses are supported by the outcome of the meta-analysis on pest insects which showed that the qualitative composition of mixed stands is of importance (Jactel and Brockerhoff, 2007). On average and for oligophagous insects, the reduction of pest damage is twice as large in mixtures associating tree species that do not belong to same class, i.e. angiosperm and gymnosperm trees, than in mixtures with only angiosperms (broadleaved) or only gymnosperms (conifers). Furthermore, in eight case studies where pure stands were compared with different mixtures with an

increasing proportion of associated tree species, insect pest damage significantly decreased with decreasing proportion of host tree species in the mixture (Fauss & Pierce, 1969; Katovich, 1992; Su et al., 1996; Nichols et al., 1999; Jactel et al. 2006).

A third type of obstacle may also disrupt the colonisation process of forest pest and pathogens in mixed stands, the phenological barrier. In several tree defoliators, young larvae can only feed on young leaves so good synchrony between tree budburst and insect egg hatching phenologies is crucial for the development of pest populations (van Asch and Visser, 2007). Similarly in some fungal pathogens, such as rusts, temporal coincidence between the emission of spores and budburst or shoot elongation is needed to succeed in infecting host trees (Blenis and Li 2005, Desprez-Loustau and Wagner 1997 a). In mixed stands, egg hatch or spore emission is then likely to misfit with bud burst or shoot elongation of at least some of the tree species, thus decreasing the rate of infection (DuMerle and Mazet, 1983). In contrast, host-specific adaptation to the narrow phenological time window is easier in pure stands, leading to improved temporal synchrony between pest and tree development and then higher risk of damage (Mitter et al., 1979).

Damage by generalist insect or mammalian herbivores on a focus tree species may also be reduced in tree mixtures where it is associated with other, more palatable secondary tree species that are exploited first. Such a diversion process has been observed in mixed eucalypt stands for *Amblypelta cocophaga* (Bigger, 1985) and *Chrysophtharta bimaculata* (Elek, 1997) by planting alternative, more preferred shrub or tree species that concentrated pest attacks. However, most often, the association of several host tree species leads to the opposite pattern, i.e. a significant increase in polyphagous pest or generalist pathogen damage in mixed stands. This process, sometimes called associational susceptibility (White and Whitham, 2000) is comparable to contagion and happens when a generalist herbivore builds up its population on a first, more palatable tree species, exploits the main part of this resource and then transfers its individuals to other host trees. In the meta-analysis comparing insect herbivory in pure vs. mixed stands (Jactel and Brockerhoff, 2007) 42 studies involved polyphagous pest insects. In 21 of these cases, no or less palatable other tree species were associated with the focus tree in the mixture and the level damaged on focus trees remained higher in pure stands. By contrast, in the other 21 studies where more palatable host trees were included in the mixture, mixed stands were more damaged overall than pure stands. Similarly, the presence of a preferred species (high quality food resource) in a mixed stand increased the level of damage on less preferred species (low-quality food) by mammalian herbivores like vole and moose (Pusenius et al., 2003; Vehviläinen and Koricheva, 2006a) or kangaroos (Pietrzykowski et al. 2003). Although less documented, an analogous contagion process is likely to apply to non

specific fungal pathogens. Developing first on more suitable (sensitive) host trees, pathogens may produce many spores that can later infect neighbouring, less susceptible, tree species. The intensity of *Armillaria* damage increased in mixed plantation with the proportion of conifers which are more susceptible species (Gerlach et al, 1997). Hansen and Goheen (2000) report the observation that pine species are rarely infected by *Phellinus weirii* in pure stands whereas they can be colonised when mixed with more susceptible conifer species such as Douglas fir. Heteroecious pathogens or pest insects such as many adelgids also benefit from tree mixtures when the latter include their two obligatory host trees. Opposite to the insurance hypothesis, the more tree species in a stand the more likely is this stand to include host tree species assemblages that meets the requirement of generalist or heteroecious herbivores and pathogens.

The second main reason for explaining why mixed stands would be less prone to pest and pathogen damage than pure stands is the enhancement of their control by natural enemies (Root, 1973; Jactel et al., 2005). Generalist predators and parasitoids would benefit from more alternative preys or host in more diverse tree communities as the latter provide habitat for more herbivorous species (Siemann et al., 1998). For example, at least three parasitoids of the spruce budworm are known to alternate on other Lepidoptera species that feed on deciduous trees (Maltais et al., 1989; Cappucino and Martin, 1997; Cappucino et al., 1998) thus resulting in higher parasitism rates of *C. fumiferana* in conifer stands mixed with hardwoods (Kemp and Simmons, 1978). Tree mixtures are also more likely to accommodate plants providing a better supply of complementary food that help adult specialised parasitoids to prolong their lifespan. The longevity is significantly increased in parasitoids of *Rhyacionia buoliana* (Syme, 1975) or *Ips typographus* (Hougardy and Gregoire, 2000) when the wasps are exposed to nectariferous flowers commonly found in conifer stands. Honeydew, commonly produced by tree aphids, is another food source for adult parasitoids. Mixed stands may provide a more consistent supply of honeydew since different tree species will host different aphid species that produce at different time (Zoebelein, 1957). Because they are structurally more complex, mixed forest also offer more shelters from adverse conditions to natural enemies (Finke and Denno, 2002) and more nesting sites to insectivorous birds (Dickson, 1979; Barbaro et al., 2007). Finally, it has been suggested that mixtures of tree species would better accommodate antagonistic fungi that slow the spread of fungal pathogens such as *H. annosum* (Johanson and Marklund, 1980; Fedorov and Poleschuk, 1981). The presence of *Acacia* species in the understorey of *Eucalyptus* forest may also increase available soil nitrogen, resulting in a more diverse microflora among which some species would exert antagonistic effects against *Phytophthora cinnamomi* (Murray, 1987).

The risk of a tree being damaged by wind depends among others on tree characteristics (especially height, diameter, vertical crown area), tree species (determining wood strength, streamlining characteristics, evergreen or not) and the surroundings of a tree (neighbouring trees providing shelter and support). Mixing trees of different species will not only influence directly the surroundings of a tree, but will also indirectly influence the tree characteristics via alteration of the competition within a stand. Replacing unstable tree species with a more stable species with exactly the same competition characteristics would then probably lead to a proportionate decrease in wind damage. However, if the more stable tree species would have a faster height growth, the unstable species would get a more sheltered position, although diameter growth might be negatively affected as well. Furthermore, belowground competition between species can alter the depth distribution of roots with either a positive or negative effect depending on species (Schmid and Kazda, 2001). The exact influence of mixing tree species will therefore depend very much on which tree species are mixed, in what proportion they are mixed, how they react to each other, and how the mixture is managed.

Conclusions

Based on much evidence, this review lends support to the hypothesis that mixed forests would be more resistant to biotic hazards than pure stands. However forest diversification cannot be seen as a panacea to control herbivores and pathogens. Several authors have pointed out that some diverse forests may be prone to pest outbreaks while some lucky monocultures can avoid health problems (for example, Pautasso et al., 2005; Koricheva et al., 2006). These apparent contradictions probably result from a lack of understanding of the ecological mechanisms underlying the effects of forest stand diversity on pests and pathogens. By exploring the relationship between forest diversity and accessibility of the host trees or the stability of natural enemy's populations, we have raised two crucial points: (1) the species composition of the tree mixture is often more important than the number of tree species and (2) the strength or the sign of the effect of biodiversity on forest resistance depends on the specialization of pests or pathogens. Basically the association of more palatable or sensitive host trees is likely to increase damage from generalist herbivores or pathogens on the focus tree species. In contrast, the addition of the largest proportion of tree species that differ greatly in their functional traits, may improve the resistance of a tree species grown in mixed stand to specialist herbivores or pathogens. The diversification of forest stands as a preventive control method should therefore be supported by a thorough analysis of hazard prevalence and focus on the optimization of tree species assemblages.

4. Genetic material

Once the tree species are chosen for afforestation, selecting adequate tree genetic material for a specific site is a key step in forest planning. Among other implications, it may prevent forest damage by favoring tree vigor or by avoiding planting susceptible species or provenances in high hazard areas to a given damage agent. Illustratively, disease avoidance through planting tolerant species in regions with high risk has considerably reduced losses due to *Sphaeropsis sapinea* in South Africa (Wingfield & Swart, 1994). However, genetic selection has been moved mainly towards increase in trees productivity and in the quality of forest products. Moreover, most breeding programs select for growth in the absence of damage (e.g. Borralho et al., 1992) which might result in selecting more productive but also more susceptible trees. Still, forest vulnerability, in particular related to intensive forestry and the invasion of exotic pests and diseases are often concern to forest health justifying the attempts on breeding for tree resistance (e.g. Salesses et al., 1993; Toda et al., 1993; Wingfield & Swart, 1994; Robin & Desprez-Loustau, 1998).

Patterns

Intraspecific variability was found in relation to damage by biotic agents such as insects (e.g. Jactel et al., 1999; Barre et al., 2002; Zas et al., 2005; Alfaro, 2008) mammals (Rousi et al., 1997; O'Reilly-Wapstra et al., 2002) and pathogens (e.g. Raddi & Fagnani, 1981; Dungey et al., 1997; Hodge & Dvorak, 2000; Carnegie & Ades, 2005; Milgate et al., 2005; Pinon et al 2005). Regarding abiotic agents, genetic variation has been found which influence risk of damage. Genetic variation in root architecture (Nicoll et al, 1995, Stokes et al., 1997), root depth (Cou tts and Nicoll 1990) , anchorage (Silen et al, 1993) and stem properties (Parr and Cameron 2004) will all influence the wind risk to a stand. Concerning fire no specific studies have been found on tree improvement for resistance against fire. However, the survival capability of a tree to fire has been related to variables such as the tree size, bark thickness, tree architecture and vigour (Ryan and Reinhardt 1988; Linder et al. 1998; Van Mantgem et al. 2003; Hély et al. 2003) all of which are at least partly under genetic control. Such genetic variation in plant resistance is an indication that breeding trees for resistance against pests, diseases or abiotic agents can be a successful field of research.

The determination of the resistance mechanism seems most relevant for a breeding program. Ideally if the resistance could be assigned to specific genes this would facilitate breeding programs and in fact most of the breeding programs that have so far incorporated tree health objectives have targeted single pest or pathogen species. Classical quantitative genetic theory assumes that resistant traits are inherited through genes at many different loci acting additively. However, most studied cases have

evidenced that plant resistance to pests and pathogens results from the combination of many mechanisms activate at different stages in the plant attack and which are likely to operate independently of each other (Carson and Carson, 1989). Moreover, the relative importance of each trait may probably change from one genotype to another and relies on the interaction between genetics and environment (e.g. King et al., 2004). Breeding programs rely on genetic prediction as measured by heritability. In many cases the expression of heritability of tree resistance was found to be low or moderate, both against pathogens (e.g. Dungey et al., 1997) and insects (Kleinhentz et al., 1998), varying from less than 0.01 to 0.5 hindering tree improvement. Higher heritability is less frequently reported (e.g. Mattson et al, 1998, Wainhouse and Ashburner, 1996; Milgate et al., 2005). In the case of pathogens, enemy “escape” has been indicated as a probably cause of low heritability, as some susceptible trees may escape disease by unfavorable conditions to pathogens, being considered as resistant. Resistance traits can be measured directly, by evaluating damage, or indirectly, using an indirect trait associated with resistance. This implies a high genetic correlation between resistance and the indirect trait. Both laboratory and field tests may be used to evaluate direct traits. Laboratory tests allow controlling variability of the pest or pathogen, not controlled when genetic materials are exposed in the field to pests and pathogens. Yet, they have size limitations regarding the number of genotypes and factors analyzed (Heidger and Lieutier, 2002). Particularly in field trials, caution must be taken to avoid conditions that favor “disease escape” which might result in taking susceptible materials by genetically resistant (Swart et al, 1996). Indirect traits may be used as markers in indirect selection programs. These markers can be biochemical, morphological, physiological or genetic. The important is that they must be correlated with the host response and resistance level (Heidger and Lieutier, 2002). As examples, the composition of terpenes might be an indicator for resistance to *D. sylvestrella* (Jactel et al, 1996), seedling color can be used as an indicator of genetic resistance to *Hylobius abietis* (Zas et al., 2005), and seedlings traits may constitute indirect traits to test potential susceptibility to wind throw (Hathaway and Penny, 1974). Selecting for leaves or needles with high surface "wettability" in tree breeding programs may also provide protection against a wide range of rust fungi by inhibiting germination and/or infection (Pinon et al, 2006, Baker et al 2006).

Major breeding programs aim to select material with higher productivity, mostly measured by growth. They rarely address resistance to insect pests and the few breeding programs that aim to improve resistance to forest diseases have mainly targeted specialised or recently introduced pathogens. As growth and susceptibility are genetically linked, there are certainly difficulties for breeding, and there is the risk that breeding for resistance could reduce genetic gains in growth. Results linking growth to susceptibility vary from no significant relation (e.g. Mitterpergher and

Raddi, 1974) towards a positive genetic correlation between tree vigor and susceptibility (e.g. Heimbürger, 1962; Jactel et al., 1996b, 1999; Zas et al., 2005). The outcome further depends on insect or pathogen specificity. Increased stem growth may also make trees more prone to wind damage if development of the anchorage system is not proportional (Silen et al., 1993; Nicoll et al., 1995), and the fastest growing trees would not be recommended for particularly exposed sites (Quine et al. 1995). In the case of herbivory it is important to distinguish the effect of vigor on resistance and tolerance. While in some cases vigorous trees may become more attractive to herbivore insects (e.g. Jactel et al., 1996b) they may also become more tolerant. Thus, selection of plants with fast growth characteristics may allow compensating damage by biotic agents through higher tolerance.

An alternative solution to improvement of trees for economic criteria while preserving tree resistance would be through hybrid breeding programs combining desirable traits, productivity and resistance (e.g. Krauss 1986; Harfouche & Kremer, 2000). However, several authors report a tendency for F1 hybrids to have susceptibility similar to the susceptible parent species and different from the resistant ones, as shown for the pine trees to *Rhyacionia frustana* damage (Highsmith et al., 2001). This may be justified by dominant genes related with tree susceptibility. Finally, enhancement for tree resistance has been attempted by transferring foreign genes that increase resistance, such as the delta-endotoxin gene of *Bacillus thuringiensis* (e.g. Tang & Tian, 2002). Similarly gene transfer from host-tree species in the native range of introduced pathogens has been proposed as a strategy to enhance resistance of tree species in the new colonised area (Adams et al., 2002)

Explanations

The susceptibility to a given pest or pathogen is usually regulated by a complex interaction of factors involving host plant (genotype and physiological state), interactions with herbivore population/strain, interactions with other biotic agents (competitors, predators, antagonists) and abiotic factors. Also, resistance mechanisms for abiotic agents such as windthrow may be complex involving several characteristics of the tree and stand (Silen et al., 1993; Kodrík & Kodrík, 2002; Stokes et al., 1997).

Tree susceptibility to pests or pathogens relies on two major mechanisms: tolerance, which reduces the loss of fitness caused by the infection or attack; and resistance, which reduces the probability of being infected or attacked (Restif and Koella, 2004). The tolerance of trees reflects their ability to

compensate damage sustaining growth and reproduction levels. Primary mechanisms of plant tolerance to herbivores involve increased net photosynthetic rate after damage, high relative growth rates, increased branching, high levels of carbon storage in roots and the ability to move carbon stores from roots to shoots after damage (Strauss & Agrawal, 1999). Both genetic and environmental factors can affect tree tolerance. Recent research indicates that there is a heritable basis for tolerance and that it can evolve in natural plant populations (Strauss & Agrawal, 1999).

Tree resistance reflects the ability to escape damage. This can result from phenological isolation, physical and chemical barriers, and deterrents or toxic traits. Phenological isolation results from differences in the life cycle of the pest and that of the plant resulting in asynchrony between plant organ availability and the activity of the insect feeding stages. Genotypes with a different phenology from the pest may then escape from the attack. This is the case of some oak species avoidance to the green oak leafroller *Tortrix viridana* by temporal mismatch between bud burst in the host and egg hatching of the pest (Heidger and Lieutier, 2002). Tree resistance to insects through physical and chemical mechanisms may be further decomposed in host selection/preference and antibiosis, i.e. traits that limit insect performance. Several studies have shown that females discriminate between host species and intra-specifically within clones or families of the same species (e.g. Pasquier-Barre et al, 2000; Barre et al., 2002). Some species are unaccepted for oviposition and therefore are non-hosts. Yet, females may further present a preference behavior among suitable host (e.g. Barre et al., 2002). Host preference might be determined by visual, tactile and olfactory signals. In particular, chemical signals emitted by plants may be determining for the insect choice (e.g. Leather, 1987). These signals may vary with genotype and plant organ (e.g. Jactel et al., 1996a; Santos et al., 2006). For example, the susceptibility of *P. pinaster* to *D. sylvestrella* was found to be related with the oleoresin terpenes composition of the trees (Jactel et al., 1996a; Kleinhentz et al., 1998). Thus, decoding signals used by the female for oviposition may be most useful for breeding programs for resistance against insects. It is anticipated that females would choose the best food sources for their offspring. However, the correlations between oviposition preference and larval performance are variable (e.g. Craig et al., 1989; Leather, 1985; Thompson, 1988; Barre et al., 2002). Selection for enemy - or competitor - free space could explain an evolutionary trend for the choice of females for suboptimal hosts. A non-evolutionary history could further explain a lack of correlation between plant choice and larvae performance. For example Barre et al. (2002) found that two non natural host plants *P. pinaster* and *P. jeffreyi* were readily accepted by *D. pini* females for oviposition but were unfavorable for larvae survival and development.

Insect performance, i.e. survival and development, is a further key factor determining the plant resistance. This relies on the capacity of the insect to cope with the physical and chemical traits of the plant. Plant primary and secondary components, in particular, determine food quality; the later may be deterrent, antifeeding or toxic. Young stages of larval development, from first and second instars, are in particular the most sensitive to food quality and less adapted to cope with toxic compounds being therefore the most important in performance tests. In some host species young larvae mortality may be higher than 90%, hindering host colonization (e.g. Hódar et al., 2002). Moreover these stages have little or no mobility and therefore can not compensate nutritional imbalance by host choice. Still, the nutritional quality of a plant depends not only on the genotype but also on plant age, phenology and environmental factors affecting its physiology and varies with the specific herbivore requirements (e.g. McClure, 1980). Constitutive defenses and induced defenses may be further distinguished. The feeding activity of insect herbivores induces direct plant defenses, involving mechanical and chemical reactions, resulting in barriers or toxic compounds that interfere with the herbivore development and may confine successful attack. Additionally, they may trigger the production of volatiles that create indirect mechanisms of defense, dissuading herbivory or attracting natural enemies of the herbivore to the infested plants (Paré & Tumlinson, 1999). There is evidence that the recognition of the attack of insects or pathogens, and the activation of specific defense responses, involve the products of several plant genes which are strongly correlated with the mode of herbivore feeding and the degree of tissue damage (Hammond-Kosack & Jones, 1996). Different modes of attack may activate different signaling pathways even in closely related insect/pathogen species suggesting that some elicitors generated by insect feeding are species-specific. Therefore, plants with high levels of induced resistance to a specific agent may be susceptible to others (e.g. Agrawal et al., 1999). Similarly, the tolerance to herbivory may also result from specific feeding mode of the herbivore (Strauss & Agrawal, 1999). The relevance of the evolution of the herbivore-plant system is well demonstrated by the interaction of *Matsucoccus feytaudi* with *Pinus pinaster*. Whereas natural hosts are tolerant or totally resistant, provenances with no previous exposure are found to be very susceptible (e.g. Schvester and Ughetto, 1986; Fusaro, 1997; Burban et al. 1999). Tree resistance to pathogens may also be broken down into steps, for example, germination, penetration in the host, and colonization of host tissues. In conclusion, resistance mechanisms are the outcome of an evolutionary history and tend to be complex and specific against a given agent.

Conclusions

Planting adequate genetic materials or using genetically improved resistant trees may make a large contribution to reducing forest damage by abiotic and biotic agents. High risk areas to a given agent are of particular interest (Wingfield & Swart, 1994). The use of intensive forest plantations that are at risk from exotic pests and diseases are the most justification breeding for tree resistance (e.g. Toda et al., 1993; Wingfield & Swart, 1994; Robin & Desprez-Loustau, 1998). Although genetic variability has been extensively reported in relation to tree resistance to pests, pathogens and abiotic agents, breeding for resistance may raise several difficulties. Resistance is commonly highly specific, necessitating breeding programs directed to a particular biotic agent. Further, heritability of resistant traits is frequently low, making the selection process difficult. Lastly resistant traits may be negatively correlated with growth or wood quality traits implying that compromises have to be made. Surprisingly, although numerous studies have dealt with tree resistance to pests and pathogens, very few tree breeding programs have included these traits. However, there are a few good examples, such as a tree breeding programmes in Europe for elm resistance to *Ophiostoma ulmi* (Pinon and Cadic, 2007) and poplar resistance to foliar rust (Berthelot et al 2005).

From the practical point of view, the measure of direct traits for resistance can be very time consuming and costly. In this respect, indirect traits may be most strategic for screening techniques in selection programs. The benefit of indirect selection can be large if the indirect trait can be easily measured and if it can be observed at an early stage of tree growth, reducing the time for breeding programs and avoiding complex, expensive and slow field tests. Ideally indirect traits should be quantifiable in seedlings. However the use of indirect selection relies on a good correlation between indirect traits and direct traits of resistance.

Anticipating what will happen with a genetically improved resistant forest plantation is a pertinent concern. The insect/pathogen response to a given genetic material is not static. Oppositely, the interaction with the plant is the outcome of a dynamic evolutionary process. Pests and pathogens may adjust their behavior to new circumstances and modify their interaction with host plants even within a few generations and in a much more rapid scale that we usually expect (Neuhauser et al., 2003). This is illustrated by the increase in susceptibility of transgenic materials resistant to insects after some generations (e.g. Frutos et al., 1999). Conservation of the genetic diversity of trees will therefore be vital, for future use in adapting forests, not only towards new products or new silvicultural practices, but also as sources of possible genetic resistant materials for when climate change, new silvicultural techniques, or introduced pests or diseases increase forest susceptibility.

5. Regeneration methods

The favoured tree species dictates to a large extent the chosen method of forest regeneration, along with site conditions and local forest practice. A wide range of applied forest regeneration methods have been applied throughout Europe due to a diversity of management aims, ranging from intensive to close-to-nature forestry. In northern Europe, replanting after clear-felling is still a common practice for regenerating a range of native and non-native forest tree species including Norway spruce, Scots pine, lodgepole pine, Sitka spruce, and genetically selected cultivars of, for example, poplar and birch. In many cases this results in uniform, even-aged stands that are potentially highly susceptible to biotic and abiotic agents. In Central Europe, due to the high proportion of protection forests in mountainous and alpine areas, there is a trend towards the maintenance of continuous forest cover over time. Given the German “Plenterwald” regime, mature individuals are removed from the stand, creating small forest gaps that are filled by natural regeneration, finally ending with multi-layered stands that have a diversity of tree species and age classes. In Southern Europe, plantation forestry based on exotics such as Eucalyptus species or introduced conifers is common, with clear-cutting and subsequent planting, but this method is also applied to native stands of maritime pine, for instance in intensively managed areas. As much of our knowledge about reforestation problems is derived from plantations, we will use this as the standard and then relate other reforestation methods to this when discussing damage problems.

Patterns

In Fennoscandia, moose damage to pine saplings is one of the most important forest protection issues, and causes annual losses exceeding 50 million Euros. In southern Sweden, many pine sites have been altered to become mostly spruce due to excessive moose damage, and in northern parts of Scandinavia much of the pine timber displays technical defects due to moose damage at the sapling stage. This problem is most pronounced in pine plantations but it also occurs in naturally regenerated pine stands, although the high stem number in such stands often allows enough trees to escape and outgrow the sensitive sapling stage. Plantations of broadleaved trees are particularly sensitive to grazing mammals, and for example, birch plantations in Fennoscandia have to be fenced during the seedling and sapling stages, greatly increasing the cost of reforestation by planting. Reimoser and Gossow (1996) recommend avoiding clearcut regeneration and instead promote the use of natural regeneration to reduce browsing damage by ungulates.

It is difficult to clearly separate the question of stand structure from that of stand composition. Regular or even-aged stand structures, are used to simplify the management of forest stands, and are most commonly applied to pure stand forestry. In contrast, mixed species stands are generally irregular or uneven-aged. Only a few studies have therefore tested the effect of stand structures, resulting from different regeneration methods, on susceptibility to forest pests for a given stand composition. Barthod (1994) and Landmann (1998) in their reviews of the question concluded that there was a lack of conclusive evidence to support the view that even-aged forests are more prone to biotic damage than selection forests or irregular stands. They cite the study from Géri (1980) who observed lower defoliation by the pine processionary moth (*T. pitycompa*) in multi-strata pine stands. They also cite Schwerdtferger (1981) and Malphettes (1977) who noticed that the aphid *Dreyfusia nusslini* and the scale insect *Cryptococcus fagi* only made significant damage in even-aged stands (high forest). However they indicate that many pest insects seem to have no preference between even and uneven-aged stands. An example in Europe is the pine sawfly *Diprion pini* (Geri and Goussard, 1984). However, in contrast, multistoried stands of conifers in North America have been observed to be more prone to defoliation by the spruce budworm *Choristoneura fumiferana* (Hadley and Veblen 1993).

In young conifer plantations in large parts of Europe, the large pine weevil, *Hylobius abietis*, is by far the most important insect pest. This problem is, however, man-made as weevil damage is closely linked to plantation forestry based on clear-felling and subsequent planting of conifer seedlings. The weevils breed in the stumps and feed on the seedlings causing annual losses amounting to tens of millions of Euros in Europe, according to a recent synthesis by Långström and Day (2002). These large losses occur despite the common practice of treating seedlings with insecticides prior to planting in order to reduce weevil damage. With the increasing concern about environmental pollution, different strategies have been developed to decrease or avoid the use of insecticides in European countries, and some countries including Germany and Switzerland have returned to forestry based on natural regeneration and avoidance of clear-felling. The use of continuous cover forestry may also help reduce the impact of pests on young trees, as shown by the reduced damage by *H. abietis* in young conifer seedlings under shelterwood (von Sydow and Örlander, 1994; Norlander et al., 2003; Pitkanen et al., 2005; Lof et al., 2005). However, because isolated trees are more prone to the pine processionary moth attacks, planting at low density may increase damage from this defoliator (Speight and Wainhouse, 1989).

Similar conclusion can be drawn about the relationship between stand structure and vulnerability to forest pathogens. The canker caused by *Nectria ditissima* appears only to be a problem in coppice,

as the few remaining infected adult trees may produce a high load of inoculum that can spill over onto beech seedlings. In contrast, such a contagion process is rarely observed after a clear cut (Perrin, 1975; Perrin and Vernier, 1979). *Heterobasidium annosum* is probably the main fungal pathogen associated with plantation forestry as it colonises stumps soon after the harvesting and then spreads to the roots of adjacent trees, killing seedlings (Woodward et al., 1998). Naturally regenerated stands are generally expected to be less infected by *H. annosum* than planted stands (Korhonen et al., 1998) and damage tend to increase with stand density. Similar observations have been made on *Armillaria* root rot infections (Morrison and Mallett, 1996). More generally artificial regeneration with pure, even-aged and dense plantations favours the occurrence and damage by *Armillaria* (Legrand et al., 2005).

It should be stressed that tree nurseries are the main gateways for the introduction of disease to forests, and therefore there is a higher risk of infection in plantations. For example *Fusarium circinatum* is the most important pathogen of *Pinus* seedlings in South African nurseries. It has been recorded for the first time in a pine nursery in 1990 and in forest plantations in 2005 (Coutinho et al., 2007). The Damping off is a common disease in seedling nurseries and may sometimes also occur at the reforestation sites. The cause of the disease is complex and many fungal species, such as *Fusarium* sp., *Pythium* sp. and *Pestalotia* sp. have been isolated from diseased seedlings. Conifer seedlings in nurseries and in the field may also suffer from “the umbrella disease”, *Gremmeniella abietina*, which is more known as the “red devil” attacking pine stands of all age classes. The most recent epidemic in 2001, covered 0.3 million hectares in central Sweden (Wulff et al. 2006). A further example is Red band needle blight infection which has recently caused wide-spread damage to Corsican pine plantations in Southern UK, the spread of which appears to have been accelerated by the use of plants infected in the nursery (Brown et al. 2003).

Spacing, either through initial spacing or due to thinning, is an important factor in determining windthrow risk. Wide initial spacing is recommended to improve stability (Bryndum, 1986; Holmsgaard, 1986; Offergeld, 1986), while close spacing is reported to be a determining factor in certain events (Soest, 1954). Wide spacing will increase the wind loading on the trees, but due to their acclimation to increased wind stress (Nicoll et al., 2008) the anchorage of the trees will become stronger. Irregular stands, such as those managed under continuous cover or Plenterwald systems, are believed by some to be more stable in strong winds than even-aged stands (Busby, 1965; Cameron, 2002), however the evidence is far from conclusive. Several authors found less damage in irregular stands (Werner and Armann, 1955; Offergeld, 1986; Dvorak et al., 2001; Schütz et al., 2006), although Cucchi and Bert (2003) found more damage in heterogeneous stands.

Schelhaas (2007) found in a modelling study the uneven-aged system particularly stable due to a strong selection pressure for the most stable trees.

It has been demonstrated that mature even-aged stands are more resistant to fire than multi-layered or young stands (Agee et al. 2000; Pollet and Omi 2002; Omi and Martinson 2004; Fernandes and Rigolot 2007; González et al. 2007b), and have lower probability of being affected by fire (González et al 2006). Thus, regeneration methods that encourage the development of even-aged stand structures (clear cuttings with planting, seed tree methods, or very intense shelterwood methods) are expected to be less vulnerable to fire. On the other hand, these methods usually involve very intensive cuttings that can produce large amounts of slash. This accumulation of dead fuel can produce a temporal increase in the risk of fire if no additional treatment is considered to reduce it (Carey and Schumman, 2003). Additionally, during early stages of development, even-aged stands can be characterized by an abundant regeneration or by the presence of shrubs due to the canopy opening, which can lead to the accumulation of very flammable surface fuels (Moreira et al., 2001; Pollet and Omi, 2002; Gonzalez et al., 2007a; Gonzalez and Pukkala, 2007).

Explanations

The effects of the type of forest regeneration on stand vulnerability to biotic hazards can be attributed to three main factors: the quality and quantity of seedlings used in planting, the succession of silvicultural operations that end up with artificial regeneration and the vertical structure resulting from the regeneration process.

Usually seedlings produced for forest plantations are grown with fertilizers in a nursery. As a result they often show vigorous growth and may better resist secondary pests and pathogens which prefer stressed trees. On the other hand young seedlings, notably when previously fertilised with nitrogen, may be also more appetizing for insect (Zas et al., 2006) and mammal grazers (Rousi et al., 1993) and more susceptible to some pathogens. For example the higher susceptibility of planted, compared to sown, pine to the twisting rust *M. pinitorqua* has been interpreted as resulting from a larger amount of susceptible tissues in the elongating shoot (Desprez-Loustau and Wagner, 1997 a,b). Several nursery practices including irrigation, fertilisation, fungicide applications and short rotations are considered as the main drivers of the persistence of asymptomatic pathogens in young seedlings. Planting these seedlings in poor site conditions may trigger the disease outbreak, thereby providing new opportunities for disease spread. Compared to natural regeneration, artificial regeneration often greatly differs by having lower seedling density. In low density plantings, the

more isolated seedlings may be more prone to shoot moths such as *R. buoliana*, or tree defoliators like *T. pityocampa* which are visually attracted by tree silhouettes against clear background (Demolin, 1969). Planting at higher densities may therefore provide an opportunity to minimise overall pest damage as the affected trees can be further thinned (Wainhouse, 2005). The combination of clear-cut harvesting and regeneration through planting offers the best conditions for development of pests and pathogens, such as pine weevil *H. abietis* and the root rot *H. annosum*, which first colonise stumps and then damage neighbouring seedlings. These two operations should therefore be separated in time or space to avoid severe damage in conifer plantations. There is no clear reason why uneven-aged or multi-storied forest stands would differ in vulnerability from even-aged or regular stands. On the one hand uneven-aged pure stands may provide a more diverse diet to different pests and pathogens and therefore may suffer from a larger array of aggressors. On the other hand even-aged stands can represent a large, stable and predictable food resource that can benefit density-dependant pests and pathogens. Anyway, whether even- or uneven-aged, a pure stand will still consist of a cohort of similar individual trees with similar functional traits so that structural diversity is less likely to be relevant for reducing stand vulnerability to biotic hazards than compositional diversity. Both Barthod (1995) and Muzika and Liebhold (2000) indicate in their review that the effect of stand structure has never been adequately addressed and that too many confounding factors, such as stand composition, history of management and site conditions, probably obscure the issue.

Quine et al. (1995) argue that more even and closely packed stands are better from an aerodynamic viewpoint to resist strong winds. However, many authors expect greater stability of uneven-aged systems due to overstorey trees becoming acclimated to the wind (Cameron, 2002; Mason, 2002). In a comprehensive review of the theoretical advantages and drawbacks of different stand structures with regards to wind stability, Dhôte (2005) suggests that even-aged forests may be more resistant because of their lower canopy roughness, better dissipation of wind energy between swinging crowns of similar heights and lower crown-exposed area. In contrast selection forests would be more wind resistant mainly due to higher individual tree stability resulting from better shape (lever arm and bole taper) and better acclimation to wind. However he concludes that these positive and negative attributes are distributed between the two types of structure and that it is therefore difficult to predict which one is the less vulnerable to forest gales.

Stand structure is linked to fire hazard through its influence on fuel availability at the crown (live and dead material in the canopy of trees), surface (grass, shrubs, litter, and wood in contact with the ground surface) and ground (duff and buried wood) levels. Modification of any of these fuel strata

by silvicultural operations will thus have implications on fire behaviour, severity and suppression effectiveness (Peterson et al., 2005). Different regeneration methods will have a clear effect on the future structure development of the stand (abundance, size and spatial distribution of the trees), and thereby on the fuel availability and fire hazard.

6. Cleaning, weed control

In intensely managed forests, cleaning and weed control are considered to be operations that improve tree growth by decreasing competition with the trees (e.g. Nowak et al., 2003; Ross et al. 2005). Depending on the techniques and the objectives, the understorey vegetation can be totally removed or some vegetation between lines can be left so that the impact on biodiversity is reduced. Commonly, the removal of understorey vegetation can be achieved through the use of mechanical operations, application of chemicals, or prescribed burning. However, such an impact on forest structure abruptly changes the environment for many forest animals. The removal of vegetation or slash might be beneficial for reasons of damage prophylaxis, e.g. regarding the prevention of forest fires, yet, it is detrimental for the natural enemy fauna of many insect pests, mostly living and feeding in the understorey.

Patterns

Several studies made in Mediterranean forests have shown that tree seedlings surrounded by shrubs are protected from ungulate herbivory. The natural regeneration of *Taxus baccata* (Garcia and Obeso, 2003), *Pinus silvestris* (Gomez et al., 2001) and *Quercus humilis* (Rousset and Lepart, 2000) were favoured by the presence of a dense understorey, particularly when shrubs were higher than seedlings. Similarly Heuze et al. (2005) observed that browsing of fir (*Abies alba*) by deer (*Capreolus capreolus* and *Cervus elaphus*) was reduced when seedlings were covered by understorey foliage. The browsing of fir seedlings by roe deer was also limited by the presence of broadleaved species in the understorey (Guibert et al., 1992). The spraying of understorey vegetation resulted in an increase in deer browsing Douglas fir seedlings (Brandeis et al., 2002) which is consistent with other studies showing that deer browse conifers more frequently after neighbouring vegetation is initially reduced (Borrecco, 1972; Black, 1992).

Competing vegetation has been observed as an important factor in population stability of some insect species such as the pine tip moths or the pine processionary moth (Geri and Miller, 1985; Nowak et al., 2003). Low levels of competing vegetation are often associated with higher tip moth

infestation rates (Berisford and Kulman, 1967; White et al, 1984; Hood et al, 1988; Ross et al, 1990; Sun et al, 1998, 2000) although several studies have produced contrary or inconclusive data regarding the effects of vegetation control on tip moth damage (Ross et al., 2005). There appear to be interactions between understorey vegetation and seedling damage caused by a major insect pest in Europe, the pine weevil, *Hylobius abietis*. Soil scarification before planting has been found to reduce pine weevil damage and the effect is most pronounced if scarification leads to a planting spot of mineral soil (Örlander and Nordlander, 2003). This effect is more evident in the first year after planting, and is greatly reduced within 2 years (Pettersson et al., 2006). An opposite effect is observed in the white pine weevil, *Pissodes strobi*, where one of the main management options to control white pine weevil include the provision of shade with nurse crops (Dixon et al, 1979; Hodge et al., 1989; Bellocq and Smith, 1995). Slash burning is recommended to prevent outbreaks of *Hylastes angustatus*, a root infesting bark beetle (Wingfield and Swart, 1994). However when not well controlled, fires may induce severe infestations of *Orthotomicus erosus* which can colonise burnt trees, build up their population and then attack healthy trees (e.g. Fernandez, 2006; Schwilk et al. 2006; Wingfield and Swart, 1994).

Concerning disease, the effect of vegetation control by fire can favour pyrophilous fungus, such as Rhizinia root disease (*Rhizinia undulata*) (Wingfield and Swart, 1994). This conifer pathogen requires a heat stimulus for the onset of pathogenicity. Shrubs species like viburnum and rhododendron in England (Brasier et al., 2005) and Bay laurel or small tanoaks in California (Maloney et al. 2005) are known to be highly sensitive to the generalist pathogen *Phytophthora ramorum* and serve as reserve of inoculum. The management of these understorey species may then reduce the inoculum pressure from the causal agents. Spraying fungicides on the understorey has been shown to enhance birch regeneration indicating that *Betula papyrifera* is probably prevented from establishing by its susceptibility to pathogens originating from understorey environments (O'Hanlon-Manners and Kotanen, 2004). Some other pathogens alternate on several hosts, including herbaceous plants or shrubs in the understorey vegetation, to complete the life cycle. Several of such associations benefit rust diseases such as on *Pinus pinaster* or *P. silvestris* and aspen seedlings, *Abies alba* and stitchworts, Poplar trees and *Allium* sp. (Nageleisen et al., 2002). The density of the vegetation is also relevant to the expression of fungal pathogenicity as some pathogens like *Lophodermium seeditiosum* in pine stands or *Phaecryptopus gaeamanii* in Douglas fir stands are favoured by bushy understorey whereas others like the mildew *Erysiphe alphitoïdes* developed better in oaks stands with no understorey vegetation (Nageleisen et al., 2002).

The removal of surface fuels, including weeds and shrubs, through mechanical or chemical processes is effective for reducing the risk of forest fires (Agee and Skinner, 2005) but the cost of such treatments is generally very high. A more cost-effective practice for reducing surface fuels is the use of prescribed fire. It has been widely studied and recommended in the USA (Cumming, 1964, Deeming, 1990, Fulé et al., 2001a, b; Pollet and Omi, 2002; Finney et al., 2005). In Europe, prescribed fires had limited importance in the past (Xanthopoulos et al., 2006). However, recent efforts have improved the scientific and technical basis for the application of prescribed burning (Silva, 1997; Fernandes and Botelho, 2004) and to predict its side effects on different ecological aspects (Moreira et al., 2003; Fernandes and Botelho, 2004).

Explanations

The management of understorey vegetation may reduce herbivory by limiting the access to food resources. First, dense vegetation or heavy slash may impede mammal herbivore movement (Emmingham et al., 1989; Rochelle, 1992) and unmanaged understorey, especially those with high concentrations of thorny species such as *Rubus* or *Ulex*, may have been simply impenetrable, even for deer. When the understorey vegetation had been removed around seedlings, they may also become more noticeable to foraging deer. Broadcast spraying increased the percent cover of herbaceous plants, grasses, and trailing blackberry (*Rubus ursinus*, a preferred winter browse species) and decreased the percentage of shrub cover (Brandeis et al., 2002). This may have encouraged deer to forage in the area. Likewise pine tip moths probably locate host tree seedlings that stand out from the understorey layer so that high vegetation may better conceal young conifer seedlings. Shelter and burrowing places in the close vicinity of a seedling should make it possible for the pine weevil to hide, rest and repeatedly return to the food source (Björklund et al., 2003). However shrubs can also provide shelters for small mammal herbivores such as hares which can seriously damage newly established conifer seedlings (Oxenham, 1983).

Second, the presence of other palatable species in the understorey may provide an alternative to planted seedlings as herbivores primarily forage on their preferred plant species. This seems to be particularly true when broadleaved shrub species are present in the understorey of conifer plantations (Guibert et al., 1992; Brandeis et al., 2002). Pine weevil apparently feed mainly on food sources other than conifer seedling (Örlander and Nilsson, 1999) and shrubs and herbs on the ground can serve as weevil food thus reducing the feeding pressure on young seedlings (Örlander et al., 2001).

However, when the preferred food resource becomes scarce, there is a risk of spillover of herbivores onto less preferred but still present host species such as tree seedlings. For several pathogenic fungi like *Phytophthora*, understorey vegetation may also serve as reservoir thus increasing the inoculum pressure on neighbouring trees or seedlings (O'Hanlon-Manners and Kotanen, 2004; Brasier et al., 2005; Maloney et al., 2005). Similarly several bark beetle species can benefit from slash to maintain population in forest stands or clearings.

Understorey vegetation may also drive microclimatic conditions that are favourable to spore dispersal and germination. Damages caused by *Melampsora larici-populina* increase with air humidity, and are therefore limited when herbaceous or shrub layers are controlled (Maugard et al., 2000). In contrast, the mildew *E. alphitoïdes* requires dry and warm temperatures to develop and is thus more frequent in low density oak stands (Nageleisen et al., 2000). Forest heteroecic rusts need to alternate between two different host plants, one of which is often present in the understorey vegetation. The survival of the spores depends on the distance between individuals of these two hosts which obviously increases following weeding operations (Nageleisen et al., 2000).

The understorey vegetation may also provide suitable habitat for natural enemies which can better control pest insects (Miller and Stephen, 1983, Ross et al., 2005). A part of the natural enemy fauna, which comprises predators and parasitoids, live and feed in the understorey vegetation, hence the importance of leaving some for the benefit of the natural enemies. It has been shown for example that removing competing vegetation in loblolly pine plantations can reduce total parasitism of pine tip moth (McCravy et al, 2001 In Ross et al. 2005).

The influence that surface fuels, i.e. living or dead ground vegetation, has on the risk of fire is clear and widely studied. The abundance of these fuels increases the probability of fire ignition, and favour an easy spread of surface fires. It determines the intensity of surface fires, and if the understorey height tends to reach the base of the canopy it can also initiate crown fires (Rothermel and Philpot, 1983; Finney ,1999).

Conclusion

There is a clear positive effect of cleaning forest stands in reducing competition for resources such as light, water and nutrient, especially for young seedlings, and to prevent forest fires. In contrast the figure is more complex regarding the effect of understorey vegetation management on biotic damage. Simply, a high or dense understorey may contribute to reducing the access of herbivores or

pathogens to host trees or seedlings and enhance their control by natural enemies providing that understorey vegetation does not accommodate other palatable or susceptible host plants that might act as reservoir and increase feeding or inoculum pressure on trees.

7. Thinning and pruning

Thinning is the mechanical removal of some trees in a forest stand. Once or repeatedly applied during the period after stand establishment and prior to final harvesting, these management operations aims at the enhancement of tree growth, vitality, as well as stem and wood quality. The type of thinning (frequency, timing, intensity, selection objectives) may change tree species composition and influence the vertical and horizontal structure of the stand. Thinning also creates stumps and dead wood. If not well performed, thinning operations can result in mechanical damage to the remaining trees, for example from felling trees or from heavy machinery on the site.

Pruning is a silvicultural tool to accelerate the otherwise natural loss of branches regulated by stand density. Trees grown at a wide spacing, retain more of their branches, and if unpruned, these grow thicker, thus reducing the quality and value of the wood through the presence of large knots. Therefore these living branches are removed, normally by saw, from the lower part of the crown. The removal of dead branches avoids the rotting of these branches on the stem, while the removal of living branches reduces the assimilating area. This can have an influence on the vigor of the tree, especially if it is combined with a thinning. Normally the pruned trees are favored in thinnings so that growth is focused on the higher quality trees.

Patterns

The opening of forests by thinning may be expected to strongly reduce the probability of bark stripping by deer, as closed and dense forest stands offer the ungulates protection against adverse weather conditions and predators (Führer & Nopp, 2001). However, in contrast, it was shown by Sullivan et al. (2007) that in Canada heavy thinning resulted in an increased abundance of deer (*Odocoileus hemionus*), and moose (*Alces alces*) in young pine stands. The density of small mammal populations (mice, chipmunks, squirrels, woodrats, voles and shrews) has been observed to increase following thinning operations in pine forests (Homyack et al., 2005; Converse et al., 2006 a, b).

Pruned trees with a thin bark are especially susceptible to bark stripping by red deer, whereas enhanced radial growth and the development of a thick bark reduces the attractiveness of stems for deer. These stem characteristics are strongly influenced by the intensity and quality of thinning operations.

During thinning operations, attacked or infected trees can be selectively removed or pruned in order to improve stand health and to reduce the risk that infestation foci expand. This so-called “sanitation thinning” is reported to be particularly effective in controlling pests and pathogens with low dispersal ability and slow development, such as some root rot fungi and sap sucker insects (Wainhouse, 2005).

Many pest insects respond positively to thinning operations. Some defoliators, including the pine processionary moth, *T. pityocampa* (Speight and Wainhouse, 1989), the pine tip moth *Rhyacionia frustrana* (Berisford, 1988 in Wainhouse, 2005) and spruce budworm, *Choristoneura pinus*, can increase their damage to trees that are better exposed to the sun after thinning (Nealis and Lomic, 1994; Kouki et al., 1997). The removal of overstorey trees during thinning also results in increased damage by the pine weevils *Pissodes strobi* (Taylor et al., 1996) and *H. abietis* (Wallertz et al., 2005). Mechanical damage caused by machinery during thinning operations has been observed to enhance attacks by several bark beetle species such as *Dendroctonus murrayanae*, *D. valens* and *D. micans* (Gregoire, 1988; Safranyik et al., 1999 in Wainhouse, 2005). Similarly pruning live branches results in higher damage on maritime pine by the stem borer *Dioryctria sylvestrella* (Jactel et al., 1994) and increases the susceptibility of spruce (*Picea abies*) and Scots pine to bark beetles and their associated fungi (Christiansen and Fjone, 1993; Solheim, 1993; Langstrom et al., 1993). Recently cut logs and branches from thinning operations constitute a major substrate for many bark beetles such as *Ips typographus*, *Trypandendron lineatum* and *Tomicus piniperda* (Speight and Wainhouse, 1989) and other *Ips* spp. In Poland, Sierpinski (1972) noticed that strongly thinned young pine stands were more prone to damage by *Exoteleia dodecella*, *Rhyacionia buoliana*, *Aradus cinnamomeus*, *Evetria resinella*, *Brachyderes incanus*, *Cacoecia piceana* and *Neodiprion sertifer*. In old stands, thinning favored the infestation by three defoliators, *Diprion pini*, *Dendrolimus pini*, and *Acantholyda nemoralis*. Likewise, secondary bark beetles such as *Phaenops cyanea* and *Ips sexdentatus* were more abundant in thinned stands. Timing of thinning is of importance. Postponing thinning operations to summer or autumn, i.e. after the emergence period of bark beetles such as *Pityogenes chalcographus* (Grijpma and Schuring, 1984 in Speight and Wainhouse, 1989) and *T. piniperda* (Bevan, 1974 in Speight and Wainhouse, 1989) can help to reduce the risk of attack in conifer stands.

In contrast, increased tree spacing after thinning reduced the percentage of trees attacked by the fir aphid *Cinara todocola* (Furuta and Aloo, 1994 in Wainhouse, 2005). Selective thinning with the removal of stressed or slowly growing trees have been shown to reduce tree mortality by the woodwasp *Sirex noctilio* in Australia (Neumann and Minko, 1981, Speight and Wainhouse, 1989). Thinning has been proposed as a method to reduce defoliation by *Lymantria monacha* in Scots pine stands (Habermann & Bester, 1997). Several authors found that thinning may reduce bark beetle attack through the decrease in competition between trees (Hard, 1985; McCambridge & Stevens, 1982; Worrell 1983). Recently Fettig et al. (2007) thoroughly reviewed the relevance of thinning to prevent and control bark beetle infestations in coniferous forests of North America. They provide a long list of studies that clearly show that thinning can be recommended to reduce the occurrence, and the growth, of subsequent infestation spots of the devastating mountain pine beetle, *Dendroctonus ponderosae* in *Pinus ponderosa* and *P. contorta* forests, as well for the southern pine beetle *Dendroctonus frontalis* in *Pinus taeda* stands.

Numerous studies have demonstrated that root rot fungi such as *Armillaria ostoyae* (Morrison and Mallet, 1996; Morrison et al., 2001; Robinson, 2003; Legrand et al., 2005) and *Heterobasidion spp.* (Piri and Korhonen, 2007; Ronnberg et al., 2006; Pettersson et al., 2003; Bendz-Hellgren and Stenlid, 1998) usually colonize fresh stumps to create new inoculum sources and spread to neighboring trees. Due to this, butt rot tends to occur in clusters (Piri et al., 1990). Second-rotation stands therefore have a higher risk of infection to thinning stumps (Stenlid, 1987; Piri, 1996; Stenlid & Redfern, 1998; Vollbrecht & Stenlid, 1999). It is generally acknowledged that the stronger and more frequently a stand is thinned, the faster is the development of *H. annosum* infection (Korhonen et al., 1998). Because there is a positive correlation between the diameter of the stump and the infection possibility (Swedjemark & Stenlid, 1993; Bendz-Hellgren and Stenlid, 1998), damage by *H. annosum* is lower for smaller stumps of precommercial thinnings (Vollbrecht et al., 1995a, Bendz-Hellgren et al., 1999). In New Zealand it was observed that a thinning operation increased the rate of damage by *Armillaria novae-zelandiae*, particularly in trees closer to fresh stumps (Hood et al., 2002). Uprooting thinned trees has been proposed to avoid the increase of *Armillaria* damage in thinned stands (Hood et al., 2002; Robinson, 2003). Thinning operations can therefore increase both the risk of establishment and expansion of the disease in conifer stands. The risk of *H. annosum* infections in a stand is also related to the amount of wounds left by a thinning (Rishbeth, 1951). Likewise root and collar injuries made during thinning operations can enhance the infection by *Armillaria* (Singh and Pandey, 1989; Bruhn et al., 2002). Machines operating within a stand can also break rhizomorphs into many pieces, each representing new sources of infection, and

thus increasing the risk of damage (Rykowski, 1985). Additionally the timing of thinning operations during the year influences the risk of an infection. If thinnings are carried out during the growing season when airborne spores are plentiful, the risk of infection is higher than in winter (Rönnberg et al., 2006).

Oak trees in coppice have been found to experience twice the damage by root rot disease compared to oak trees of the same diameter in high forests, largely because of stump infection during the coppicing operations (Piou et al., 1997). Some forest pathogens first infect branches before spreading through the stem and causing cankers. It has been shown for example that pruning branches infected by the blister rust *Cronartium ribicola* significantly reduced the rate of mortality of white pine (Hunt, 1991). In contrast severe pruning of *Pinus radiata* can result in higher mortality due to an increased susceptibility to *Armillaria* (Hood et al., 2002) or infection by *Sphaeropsis sapinea* (Chou, 1988)

Generally, mature even-aged stands have lower probability of being affected by fire than multi-layered or young stands (González et al., 2006) and are more resistant (Agee et al., 2000; Pollet and Omi, 2002; Omi and Martinson, 2004; Fernandes et al., 2006; González et al., 2007b). Stands with higher tree density are also more vulnerable to fire (Kalabodikis and Omi, 1998; Pollet and Omi, 2002; González et al., 2007). In this context, it can be said that thinning regimes that reduce fuel loads in the forest, especially thinnings ‘from below’, are of great help in reducing the risk and intensity of crown fires (Graham et al., 1999; Fulé et al., 2001a, b; Pollet & Omi, 2002; Peterson et al., 2005; Agee & Skinner, 2005). As the smallest trees are removed, the remaining larger trees have thicker bark and a higher canopy, reducing the potential severity of damage by fire and the risk of a crown fire ignited by torching. Another advantage of such treatments is that they provide better and safer access for firefighters if required. Thinning from above, focused on the removal of dominant and co-dominant trees, has also been suggested (Graham et al., 1999; Fitzgerald, 2002) as a method to develop fire-resistant stands. The release of competition, and growth enhancement, of suppressed trees lead to mature regular stands, with higher revenues from the thinnings. However, the use of thinning from above implies that the stand will reach the mature stage later than with the use of thinnings from below. Therefore, the stand may be subjected to higher levels of risk during longer periods. An additional management option that may be considered to strengthen the effect of thinning is pruning, to reduce the amount of canopy fuel and increase the canopy height.

Thinning has a well known negative effect on stand stability to strong winds in the first years after a thinning (van Soest, 1954; Werner and Armann, 1955; Van Nispen tot Sevenaer, 1975; Nielsen,

1986; Savill, 1983; Miller, 1986; Lohmander and Helles, 1987; Quine et al., 1995; Schreiner et al., 1996). The negative effects of thinning are reported to increase with thinning intensity and age of the stand (van Soest, 1954; Bryndum, 1986; Eriksson, 1986; Holmsgaard, 1986). In general, selective thinning is considered to be less stabilizing than systematic thinning (Cremer et al., 1982; Touzet, 1983; Bryndum, 1986; Eriksson, 1986; Holmsgaard, 1986; Ni Dhubhain et al., 2001; Cameron 2002). However, selective thinning can be implemented in different ways, where removing dominant trees is thought to be more destabilizing than removing suppressed trees (Nielsen, 1995; Ruel, 1995; Cameron, 2002). The negative effect of a thinning generally lasts a few years (van Soest, 1954; Holmsgaard, 1986; Lohmander and Helles, 1987; Urban et al., 1994; Schreiner et al., 1996; Cameron, 2002), but can last up to 10 years (Werner and Armann, 1955). However, in the medium to long term, thinnings do have a positive effect on stand stability because individual trees adapt their anchorage to increased wind exposure (Eriksson, 1986; Nicoll and Ray, 1996; Cameron, 2002). In Sitka spruce/Scots pine mixed stands, the risk of wind damage can be reduced by the enhancement of structural diversity with appropriate thinning (Mason and Quine, 1995). Wind risk is the main limiting factor for transformation towards continuous cover forestry (Mason, 2002) in the windier parts of Europe. Such transformations should therefore be started at early age, as risk will be too great in older stands (Hale et al., 2004). On sites where thinning is not an option, the use of a self-thinning mixture is a possible alternative (Savill, 1983; Quine et al., 1995; Ruel, 1995), although it would not always be appropriate (Cameron (2002) and Schelhaas (2007)). Thinning also can have an indirect negative effect on stability by promoting infections with butt-rot (*Heterobasidion annosum*), which weakens root and stem resistance. Holmsgaard (1986) states that heavy thinning often leads to a high butt-rot frequency and stresses the strong correlation between butt-rot occurrence and windthrow. Additionally, damage to the remaining trees due to thinning activities can increase the rates of fungal infection (Schmid-Haas and Bachofen, 1991).

Explanations

There are several direct and indirect effects of thinning which influence the risk of pest and pathogen damage.

Firstly, thinning operations can change the microclimatic conditions of the stand. Increased temperatures in thinned stands may accelerate the development of certain bark beetle species and force them to overwinter in stages that are more susceptible to freezing (Amman, 1973, 1989; Fettig et al., 2007). In contrast higher temperatures may lead to a larger number of generations or sister broods in the warm season (voltinism), increasing the risk of damage. Similarly removal of

overstorey trees during thinning reduces shade conditions that are detrimental to *Pissodes strobus* development (Taylor et al., 1995). More turbulent winds may also disrupt aggregation pheromone recruitment during initial phases of host tree colonization, thus reducing the risk of mass attacks on standing trees. Thinning by providing warmer, sunnier conditions, increases the risk of infections by *H. annosum* (Yde-Andersen, 1962; Isomäki & Kallio, 1974; Kallio, 1970; Solheim, 1994; Brandtberg et al., 1996; Thor & Stenlid, 2005). Therefore it is recommended to thin during the winter when no air-borne *H. annosum* basidiospores are present (Rönnerberg et al., 2006). Möykkynen & Miina (2002) were able to optimize the management for butt-rotted Norway spruce stands and recommend thinnings during the winter with low to moderate intensity.

Secondly, thinning or pruning may open several routes for infection or attack by pest or pathogens. Fresh stumps and logging scars are especially favorable to spore infection by *H. annosum* that can subsequently spread to neighboring trees through root contacts and grafts (Korhonen et al., 1998). Stumps created by thinning operations are easily infected and provide the most suitable conditions for development for *Armillaria* root rot (Legrand et al., 2005). Stumps therefore act as both sink and source of inoculum as they represent a pathway for colonization and a breeding substrate to develop and produce new infecting spores or mycelium. Likewise, slash produced by thinning or pruning operations offer a breeding substrate for some small bark beetle species such as *Ips pini* (Gara et al., 1999; Six et al., 2002), *Hylastes angustatus* or *Pityogenes chalcographus* which can build up their population on woody debris and then attack living trees. Mechanical damage during thinning operations creates wounds that provide entry sites for many stains and rot fungi (Metzler, 1997; Hessburg et al., 2001; Vasiliauskas, 2001 in Wainhouse, 2005). However tree species are unequally vulnerable to such infections through wounds, and for example, silver firs are reported to be less sensitive than spruces (Kohnle and Kaendler, 2007). Pruning living branches may also result in higher release of volatile resinous chemicals that act as an attractant for the stem borer *Dioryctria sylvestrella* (Jactel et al., 1994). *Ips typographus*, can also be attracted by the bark odours released from residual wood after pruning or thinning and then attack living trees in the vicinity (Vaupel et al., 1981). Similarly *Dendroctonus micans* is attracted to fresh wounds made during thinning operations (Grégoire, 1988). In contrast however, as thinning results in wider spacing between trees, the risk of infection may be limited accordingly. Several authors have shown that patches of bark beetle infested trees within a stand are less likely to expand if the distance between remaining trees is increased (Gara and Coster, 1968; Johnson and Coster, 1978) although this effect is insignificant when bark beetle populations build up to epidemic level (Preisler and Mitchell, 1993). Increasing the spacing between trees may be more effective in reducing infestation by less mobile pests, for example species with wingless females (Wainhouse, 2005).

Thirdly, thinning improves individual tree vigour which can in some circumstances reduce tree susceptibility to a number of secondary pests and pathogens. The rate of tree growth can affect the resources available for defence, because both cell multiplication and defensive compound (such as secondary metabolite) production are carbon demanding, and are in competition for the carbohydrates produced by photosynthesis (Wainhouse, 2005). According to the Growth Differentiation Balance Hypothesis (Herms and Mattson, 1992, 1994) there is a physiological trade-off between growth and secondary metabolism, and a parabolic response of secondary metabolism to variation in resources availability. With low levels of resources, photosynthesis is impeded leading to a reduction in both tree growth and secondary metabolism. However photosynthesis is less sensitive to resource limitation than tree growth, so at intermediate levels of resource availability, excess carbohydrate production may be diverted to the production of secondary metabolites. Growth and defence are therefore positively correlated. When resources are particularly abundant and net assimilation by the tree crown is not limited, tree growth is favoured and secondary metabolism is reduced; the two processes showing a negative correlation, or “trade-off”. A large part of individual tree resistance to bark beetles depends on secondary metabolites. Beetles that initiate host selection are often killed by drowning or immobilization in resin exuded from entry holes; the so-called “constitutive resistance” (Lorio and Hodges, 1968; Hodges et al. 1979, Raffa and Berryman 1983, Lieutier 2005). Bark beetles that are not killed or repelled by this primary resin flow tunnel through the inner bark to construct a maternal gallery where they lay their eggs. Their action induces a wound response in the phloem that stimulates a local synthesis of secondary resin which accumulates terpenic and phenolic compounds (Lieutier, 2005). These secondary metabolites further limit feeding by bark beetle adults and offspring and also act as a barrier for the infection by associated fungi. When applied in appropriate conditions, thinning can therefore improve individual tree resistance to bark beetle through the enhancement of secondary metabolism. Similar explanations have been provided to relate thinning or pruning to higher tree susceptibility to *Armillaria* (Legrand et al., 2005). Repeated thinning operations in coppice stands (Stiell and Berry, 1986; Stanosz and Patton, 1987) or severe pruning (Hood et al., 2002) resulted in lower individual tree vigour and increased root rot damage. However, the overall negative effect of thinning of conifer stands vulnerability to *H. annosum* may be partly compensated by higher individual tree vitality, particularly in young stands where the inoculum pressure remains low (Filip, 1993 in Woodward et al., 1998).

Finally thinning can also modify the horizontal structure and composition of the forest. The effect on stand vulnerability of reducing tree species diversity was previously discussed in the "stand

composition" section. Among the explanations for higher resistance of mixed forests, the improvement of biological control by natural enemies may be of greatest importance. Weslien & Schroeder (1999) found that the number of predators of the spruce bark beetle, *Ips typographus* were significantly higher in unmanaged stands than in thinned stands, while there was no correlation between the population levels of their prey and the management intensity. Further information on this is provided by Chandler, 1987; Chandler & Peck, 1992; Økland et al., 1996; and Martikainen et al., 2000).

Explanations for abiotic risks associated to stand thinning are somewhat different. Stand structure is linked to fire hazard through its influence on fuel availability at the crown (live and dead material in the canopy of trees), surface (grass, shrubs, litter, and wood in contact with the ground surface) and ground (duff and buried wood) levels. Modification of any of these fuel strata by silvicultural operations will have implications for fire behaviour, severity and suppression effectiveness (Peterson et al., 2005). One of the principles of forest fuel reduction treatments is to decrease crown density to reduce crown fire potential. As forest thinning achieves this, it can successfully decrease the potential for fire transmission between adjacent tree crowns (Agee and Skinner, 2005).

However, reducing the accumulation of living fuels and breaking their vertical continuity may not be enough to reduce the risk of forest fire. Thinning aims to reduce the amount and continuity of standing vegetation, but may produce an increase of dead surface fuels (slash) that enhance the risk of forest fires (Carey and Shumann, 2003). Thinning increases surface fuel and decreases the moisture content through increased light and surface wind speed. The increased light availability at the forest floor also supports the growth of herbs and shrub fuels. In some cases a prescribed burning after a thinning may be necessary to reduce surface fuel (Agee & Skinner, 2005; Peterson et al., 2005; Fulé et al., 2001 a,b). However, this should not be carried out in dense forests where an increased risk of fire is evident (Pollet & Omi, 2002), and here only a mechanical low thinning should be applied. Other management operations that reduce the amount of thinning residues are recommended to make thinning more effective in reducing fire risk (Pollet and Omi, 2002; Peterson et al., 2005, Kalabokis and Omi 1998). Thinning alone may also increase wind movement and fuel drying, and this will aggravate surface fire behaviour (Pollet and Omi, 2002; Fernandes and Rigolot, 2007). One of the principles for forest fuel reduction treatments is to increase height to live crown, to reduce the likelihood of flame length attaining the tree crown (Agee and Skinner, 2005). It is widely recognised that the initiation of passive crown fires (torching) depends not only on the flame length of surface fires, but also on the base of the canopy height (Van Wagner, 1977; Graham et al., 1999; Scott and Reinhardt, 2001; Agee, 2002; Cruz et al., 2003) and the moisture of those

fuels on the lower part of the tree canopy. Two clear management options can be used for raising the base of the canopy height, the previously mentioned thinning from below, and the more obvious application of pruning.

As well as modifying the vertical and horizontal structure of a forest, thinning also affects the spatial structure. A variable-density thinning combined with both a thinning from below, and patch thinning creates heterogeneity of the canopy that results in a decreased risk of a crown fire spreading (Peterson et al., 2005). Shaded fuelbreaks (spatial buffers), which are thinned to reduce crown fuels and treated to reduce surface fuels, are common tools to reduce fire risk on a landscape level. The fire risk can be reduced by removing non-fire-resistant species, and this is especially important when thinning shaded fuelbreaks (Agee et al., 2000).

Canopy opening causes the greatest increase in risk of wind damage to forest stands. This is because a thinned stand, at least for the first 3-5 years after thinning, has increased canopy roughness (Dhôte, 2005; Schutz et al., 2006), allows the wind to penetrate the canopy, and less wind energy is dissipated by the mechanical contact between crowns (Milne, 1991). In addition, trees grown in dense stands are poorly adapted to wind movement and therefore have poor anchorage strength until they can respond to the increased wind loading by strengthening their stems and root systems (Nicoll and Ray; 1996; Stokes et al., 1997; Schutz et al., 2006; Nicoll et al., 2008). When the canopy closes again, crown contact will be restored again, allowing energy to be transferred between trees. However, after crown closure individual trees will receive less wind loading, and the positive effects of the thinning will gradually decline. It is also important to consider which trees are removed in thinning. Selection based on stem form may leave the most stable trees, but thinning from above can result in removal of the more stable trees (Cameron, 2002).

Conclusions

Thinning can produce a cascade of effects on stand vulnerability to biotic and abiotic hazards, through the modification of the microclimate, changes in shape and vigor of remaining trees, and via the provision of food or shelter for beneficial or damaging organisms associated with dead wood and stumps.

There are many dimensions of a thinning which influence the risks to a stand, including thinning type, intensity, timing, and the interactions with other forestry practices such as slash or understorey

management. Their individual importance varies depending on the agent. While for example the type and intensity of thinning are particularly important in assessing the risk of fire, the timing of thinning is of particular importance for assessing the risk of fungi infections. It is therefore difficult to assess the “total” or “global” vulnerability when taking the different agents, and especially when taking their different levels of damage, into account. It should be remembered that not all hazards are fatal to the trees and for example, some only change the quality of the wood or the rate of growth. Therefore the most important issue to resolve before assessing the impact of a thinning on risk to a stand has to be the base unit to compare it to. The base unit may be mortality, or alternatively may be economic or biodiversity loss. There is no one thinning regime which lowers all risks, but there must be careful consideration of which are the most important risks to be managed. It may be possible to reduce a combination of risks by choosing an optimal thinning regime, however it will be important to take into account that other combinations of risks may have contrary thinning requirements. Therefore an optimal thinning regime should be adapted to the local situation and should balance requirements for the management of the different risks depending on the local objectives.

8. Harvesting and tending

The development of forests managed with the objective of wood production is terminated by harvesting operations, which from a technical point of view, is a sequence of cutting, processing and transport of timber. However, as forests are not only timber factories, but combinations of living organisms, logging should also be seen as a silvicultural operation that intervenes in the forest ecosystem and abruptly changes its ecological characteristics. The scale of this impact, for example, the effect of mechanical injuries on the predisposition of residual trees to damaging agents, relates to the applied method of harvesting (clearcut, selective cutting, shelterwood, etc.), its intensity (volume of logged trees), the type of machinery used, the rotation length and yield age, and the time of logging in the season.

Patterns

Very little specific information is available about the possible effects of final harvesting operations on the damage caused by game and grazers in European forests. Data from North American forests indicate that overall, clear cutting is favorable to deer, moose, hares and rabbits (Harlow et al., 1997) providing that nearby shelter against adverse weather conditions or predators is available.

Partially harvested stands show higher abundance of deer mice than un-harvested stands but the difference was not significant for voles and shrews (Fuller et al., 2004). The diversity of harvesting practices such as clear, selection or retention cutting creates a landscape mosaic of structurally different stands that are favorable to moose (Monthey, 1984). For European forests, Reimoser and Gossow (1996) suggest a gradient of red deer response with highest predisposition to bark stripping in the case of clear felling and artificial regeneration, medium predisposition in the case of natural regeneration under shelterwood and low predisposition in the case of natural regeneration combined with selective cuttings or cutting of only very small gaps.

Spruce roundwood stored in the forest is a potential breeding site for wood-damaging insects. Therefore the risks should be considered in deciding on the timing of removal from stands and in the selection of storage sites outside the forest (Capecki, 1976). Pine roundwood felled in summer should not be stored, with bark still attached, in the forest for more than 4 weeks because of the risk of bark beetle infestations (Koehler and Kolk, 1974). Most of the living trees attacked by *Ips sexdentatus* following the 1999 storm in a maritime pine forest were located in the vicinity of logs stored along the roads (Samalens et al., 2007). Logs infested by bark beetles should where possible be debarked to minimise the risk (Dehlen et al. 1982, Dubbel 1993, Wilczok 1975). In contrast, the debarking of stumps appears not to affect *H. abietis* occurrence (Elton, 1964). Removal of logging residues is also crucial in reducing the risk of an increase in the population density of bark beetles that feed on conifers, especially *Pityogenes chalcographus* on Norway spruce (Grodzki, 1997), some bark beetle species on Maritime pine (*Ips sexdentatus*, *Tomicus piniperda*, *Orthotomicus erosus*) (Maugard and Fraysse, 2002) and *Monochamus alternatus* – a vector of the pinewood nematode *Bursaphelenchus xylophilus* (Lai et al., 2001). Intensive selective harvesting in beech forests increases the risk of damage caused by wood-boring insects *Trypodendron domesticum*, *Agilus viridis*, *Taphorynchus bicolor* and *Hylocoetus dermestoides* and the immediate removal and processing of harvested wood (“clean management”) is necessary to avoid more extended damage (Losekrug, 1988; Schönherr and Rossler, 1983). Fresh beech wood left in the forest may be used as breeding material for *T. domesticum* (Petercord, 2002; Petercord, 2005) – a serious pest affecting harvested wood quality. Also stand edges, suddenly opened during harvesting, are more susceptible to mass attacks of the beech bark beetles – *T. bicolor* and *A. viridis* (Delb, 2004). Felling of beech trees infested by *A. viridis* is the recommended control method (Kamp, 1956). The timing of felling within the year is one of the most important factors influencing larval development, distribution and abundance of great pine weevil *Hylobius abietis*. Adults lay eggs in the large roots of fresh stumps in spring, and winter harvesting therefore increases the damage to Scots pine and spruce (Korczynski, 1984; Moore, 2004; Moore et al., 2004). The time of harvesting is also very important

for the risk of later infestations by bark beetles. For Scots pine the period of high risk extends from May to late August with a maximum in June-July (Koehler and Kolk, 1974). In spruce stands the timely removal of trees infested by bark beetles (“sanitation cuttings”) is crucial to avoid the risk of heavy bark beetle infestations (O'Neill and Evans, 1999; Wermelinger, 2004). However, the use of clear-cuts and the resulting creation of open stand edges can contribute to more dramatic bark beetle outbreaks (Grodzki et al., 2006; Peltonen and Heliövaara, 1999). In the case of burnt forest areas, the most severely damaged trees should also be harvested immediately in order to prevent their colonization by bark beetles (Fernandez, 2006).

Damage to planted conifer seedlings by *H. abietis* is considered to be less severe in shelterwoods than in clear-cuttings (von Sydow and Örländer 1994; Petersson and Örländer, 2003; Nordlander et al., 2003; Wallertz et al., 2005). Green tree retention is therefore recommended to reduce the damage caused by *Hyllobius* on pine seedlings (Pitkanen et al., 2005). However, this method does not automatically affect populations of *Tomicus* spp. more than traditional thinning and clear-cuttings do (Martikainen et al., 2006).

Mechanical injuries caused by machinery during harvesting operation may favour attacks by several bark beetle species such as *Dendroctonus murrayanae*, *D. valens* and *D. micans* (Gregoire, 1988; Safranyik et al., 1999). Stand vulnerability to Gypsy moth defoliations is increased by factors that reduce stand vigor such as compacted soil during logging operations. Bark beetle populations can also build up following clear-cutting or thinning operations that compact soils or wound trees.

Reduction of forest rotation length by anticipating the final harvesting may help reduce attacks by pests that mainly damage mature or over-mature trees (Wainhouse, 2005) such as some pine defoliators (Conway et al., 1999), or bark beetles such as *Dendroctonus micans* in Sitka spruce (Speight and Wainhouse, 1989) or *Ips typographus* on Norway spruce (Grodzki et al., 2006).

The transport of harvested wood across Europe increases the risk of transition of insect pests and diseases from already affected areas to the new ones. Good examples of such threats are *Matsucoccus feytaudi* in Italy (Covassi and Binazzi, 1992) or *Dendroctonus micans* in the UK (O'Neill and Evans, 1999). The improvement of sanitary felling and handling techniques in pine forests will be required to prevent the spread of *Bursaphelenchus xylophilus* (Lai et al., 2001).

Removal of stumps during or after harvesting is a recommended method to prevent the later infestations of young plantations by root fungal diseases (especially *Armillaria* spp., and *H.*

annosum) (Maugard and Fraysse 2002). Live stumps, that can still be present more than 2 years after felling, are considerably more vulnerable to infection by these pathogens than dead ones (Redfern, 1982). As young spruce trees planted on clear-cut areas already infected by *Heterobasidion* fungi are effectively infected in early phases of their growth (Piri, 2003), the optimization of silvicultural measures (including harvesting) has the potential to decrease the transfer of *H. annosum* to future generations of forest (Moykkynen and Mina 2002). The stumps in clear-cut areas are less important for the further spreading of *H. annosum* in stands than the stumps resulting from thinning (Bendz-Hellgren, 1997; Bendz-Hellgren and Stenlid, 1998).

Clear-cuts, and the resulting creation of artificial stand edges, positively influence the occurrence of wood-rotting fungi in beech, by the fragmentation of forest areas and the extended effect of “new” forest edges (Siitonen et al. 2005). The infection by *Nectria ditissima* canker is widely spread in stands which have been shaded by older trees for several decades, and selective harvesting from above may reduce this risk (Klein, 1997).

Damage caused by logging operations to spruce roots, opens new infection gates, and may be extensive at clear-felling. However, the stump surface is a much more important infection gate for *H. annosum* than root injuries (Rönnerberg, 2000). For this reason, the use of biopreparations containing *Phlebiopsis gigantea* spores on the surface of fresh stumps during or just after harvesting is a recommended method of controlling this disease (Sierota, 1995). Mechanical injuries to roots in the upper soil layer during harvesting and logging should be avoided or minimized to reduce *Armillaria* root disease (Zolciak and Sierota 1997, Bruhn et al. 2002). Mechanical injuries in the bark increase the level of red-colored heartwood in beech (Knoke and Wenderoth, 2001).

It has been proposed that shortening the rotation length of spruce forests with premature clear felling to reduce the economical impact of *H. annosum* (Korhonen et al., 1998). In contrast, premature harvesting will not prevent increment loss of pine trees infected by *Sphaeropsis sapinea* (Zwolinski et al. 1990).

Tree felling affects forest structures in both vertical and spatial aspects, but these altered structures are more susceptible to wind damage (Gardiner and Quine, 2000, Dobbertin, 2002). The greatest increase in wind risk is where forest edges are removed to expose previously sheltered trees (Mayer, 1977; Zajączkowski, 1991; Gardiner and Quine, 2000). Large clearfell areas would be better as they have relatively less edge (Savill, 1983; Quine et al., 1995). However, there would be even greater benefits of using cuts as small as 0.1 ha which would be too small to increase wind risk to adjacent

edges (Huggard et al., 1999). Many authors, for example, Faber and Sissingh, 1975; Eriksson et al., 1986, advise that felling coupes should progress in the windward direction to minimise the risk of windthrow on the newly cut stand edge. The method of stand rejuvenation is known to influence the wind stability of forest stands. In particular, methods, such as the shelterwood system, the seed tree system (Persson, 1975) and the strip cut system (Van Nispen tot Sevenaer, 1975), that retain trees from the old stand, will increase the risk to the new stand. Soest (1954) reported an increased vulnerability of stands planted under shelter. On the other hand Langvall and Örlander (2001) report, that with the clear-cut harvesting system, leaving a dense pine shelterwood led to a decrease in the damage caused by early summer frosts in Norway spruce seedlings. The reduction in stand susceptibility to windthrow can thus be achieved earlier, by forest management, mostly by focussing on rotation age and thinning strategy (Quine et al., 1995; Thorsen and Helles, 1998), and wind risk decision support systems have been developed to aid such forest management decisions (Gardiner et al., 2000). Many authors report relative higher windthrow in older age classes (for example, Putz, 1968; Grayson, 1989; Studholme, 1995; Winterhoff et al., 1995; Becker and Schröter, 2000), but this largely reflects the increase in risk with tree size (Gardiner and Quine, 2000). Savill (1983) argues that renewed attention to forest normality could be an effective option in spreading risk by reducing the proportion of stands at risk at any one time. The use of GIS-based models of the relationships between harvesting and wind risk aid the planning of forest management in the areas susceptible to direct wind action to avoid extended damage (Schmidt et al., 2006; Wichmann and Ravn, 2001).

The effect of harvesting on the risk of fire does not depend only on the number and size distribution of remaining trees (Gonzalez et al., 2007b), but also in the amount of logging slash resulting on the harvesting operations, and in the shrubs and seedlings that are recruited within the stand thanks following the opening of the canopy cover. Overall the risk of fire increases after most harvesting operations.

Explanations

The impact of harvesting on the threat from game, insect pests and fungal pathogens results mainly from the provision of food resources or accessible breeding material. In the years after clear-cutting deer food such as succulent stems of bush plants, herbs and grasses increase in abundance and availability (Harlow et al., 1997). Overstorey reduction results in increased; succulent (shrub) browsing by moose (Monthey, 1984), winter browsing (seedlings or saplings) by hare (Harlow et

al., 1997), and tree seeds and invertebrate preys for small mammals (Fuller et al., 2004). Similarly, felled trees or logging residues can serve as a breeding substrate for many bark beetles such as *Ips typographus* and *Pityogenes chalcographus* (Göthlin et al. 2000, Eriksson et al. 2005, 2006, Grodzki 1997, Grodzki et al. 2006). The seasonal timing of harvesting is therefore important for the suitability of logging residues for bark beetles. If harvesting is conducted in winter, logging residues often do not dry out and therefore remain as suitable breeding substrates for many bark beetles when they emerge from over-wintering. If brush is produced in late summer it can dry considerably faster, thus limiting the risk that the bark beetle population builds up to epidemic levels and attacks living trees (Wainhouse, 2005). Likewise, stumps of trees infected by *H. annosum* (Korhonen et al., 1998) or *Armillaria sp.* (Legrand et al., 2005), and left after final harvesting, represent important infection sources in the following tree generation. By analogy, one could also argue that harvesting operations increase the fuel to sustain forest fires. If no post-harvest fuel treatment (slash removal and bush control) is undertaken, highly flammable fuel combinations persist for several years (Weatherspoon and Skinner, 1995).

The second mechanism that relates harvesting practices to increased biotic risks originate in mechanical injuries caused by the machinery. Several bark beetles such as *Dendroctonus micans* (Gregoire, 1988) and the stem borer *Dioryctria sylvestrella* (Jactel et al., 1996) are attracted by resin odors released from bark wounds and then preferentially infest injured trees. Mechanical injuries on roots and stumps open the infection gates for root rot fungi like *Armillaria spp.* and *Heterobasidion annosum*. As a result, harvesting operations can influence the risk to stands established on already harvested areas. Mechanical injuries to roots in the upper soil layers during harvesting and logging also stimulate the spread of *Armillaria* root disease, by the stimulation of the growth of cut rhizomorphs (Zolciak and Sierota, 1997).

The third main mechanism contributing to the effects of harvesting on forest health relates to the alteration of stand environmental and physical conditions. In stands of deciduous trees, especially those with thin bark such as beech, the effect on tree physiology of suddenly opening stand edges may increase their susceptibility to pest (Delb, 2004) and fungal diseases (Klein, 1997). Additionally, the increase of solar radiation and wind circulation at ground levels may facilitate the reduction of moisture in dead fuels that facilitates the ignition and fast spread of forest fires (Rothermel and Philpot 1973, 1983). Clearfelling of a stand will also suddenly expose the edges of nearby stands to the wind, and will increase the wind speeds experienced by the trees, thus increasing the risk of windthrow. In partial harvesting, the vulnerability of the remaining trees increases due to a loss of cohesion of the stand. The remaining trees experience more wind, while at

the same time they lack mutual support. Rotation lengths influence windthrow risk in two different ways. Firstly, the older trees get, the taller they become, and thus they will receive higher wind loading and will have a longer ‘lever-arm’ (Zimmermann, 1985; Mosandl and Felbermeier, 1999). Secondly, a longer rotation increases the chance that a severe wind storm will occur (Quine et al., 1995; Schelhaas, 2007).

Conclusion

Overall it is clear that harvesting is a critical silvicultural operation with regard to risk, and results in higher risk of damage from both biotic and abiotic causes. Changes in forest stand composition and structure may affect the survival and abundance of game, insect pests and pathogenic fungi as well as their rate of development. They also trigger microclimatic changes that can enhance wind and fire damage. However two additional dimensions have to be taken into consideration. First the choice of harvesting method may have a short-term influence on stand vulnerability, due to the type of breeding substrate that is produced. Special attention should therefore be paid to possible movements of pest insects and diseases from past affected stands to newly established stands in the same area. But harvesting also has longer-term effects, as it constrains subsequent forest management, such as the choice of regeneration. Second it is not only the local scale, but also the landscape scale, which is relevant to the impact of harvesting practices. The vulnerability of stands to damage by wind, insects and diseases may be highest in the stands adjacent to recently harvested stands. Additionally, the variety of harvesting practices used in the forest landscape can also result in an increase in diversity of habitats, leading to more stable populations of natural enemies. According to the ‘insurance hypothesis’, a diversity of harvesting timing and intensity will spread the risk of damage.

9. Synthesis

What emerges from this collection of observations and explanations is that forest management substantially affects stand vulnerability to many biotic and abiotic hazards that threaten the productivity and the sustainability of forest ecosystems. However the reader of this review may get the impression that different silvicultural operations, and even different options for each of these operations, will have multiple yet contradictory effects on stand vulnerability to various hazard types. This feeling reflects the complexity of managing forests, which are in fact structurally diverse and perennial ecosystems with an almost infinite number of species interactions. It is therefore

unrealistic to search for a unique model of forest stand management that would reduce all of the risks of all types of damage, in a given situation. But fortunately this would never in practice be required as forest managers do not have to deal with such a large diversity of tree species, management options and hazard types. Foresters most commonly have at their disposal a limited number of tree species that will grow in local site conditions and the regional prevalence of hazards makes it possible to rate the main risks of damage. To minimize the vulnerability of stands to these hazards, forest managers will then have to find the best compromise between a limited set of options in the course of their silvicultural itinerary, and our review provides information that should help in the decision making process.

However, beyond this case-by-case and step-by-step approach, we believe that it is possible to draw out general conclusions that hold across a wide range of forest conditions. Going back to our explanations of the effects of silvicultural operations and options on stand vulnerability, we have identified *four main processes* that drive these causal relationships.

First of all we described *individual tree physiology and development* as being the main factor in resistance to various hazards. The palatability of tree tissues, the amount of secondary metabolites, and the phenology of growth, are the main drivers of tree susceptibility to mammal grazers, pest insects and pathogenic fungi. The size and shape of trees, and the root development are particularly important in predicting the resistance to strong winds. The water and biochemical content of tree component parts also determine tree inflammability. All of these individual attributes depend on tree phenotype, which results from genotype \times environment interactions. If a particular tree species is to be grown, the selection of appropriate genetic material, and the local site conditions, are both important in tree resistance to the main local hazards. Later in the course of the silvicultural itinerary, site preparation with direct effects, through operations such as scarification or fertilization, stand composition through the interactions between tree species, the type of regeneration, and the thinning regime that drives competition between trees for light, water and nutrient resources, can all greatly influence individual tree growth and metabolism, and thus modify their susceptibility to biotic and abiotic hazards. It is important here to remember that optimizing tree growth will not necessarily improve tree resistance as some primary pests and diseases may develop better on vigorous trees, and similarly, the more productive stands may be more sensitive to strong storms or fire hazards.

Second, we described *local microclimate* as being not only an influence on tree physiology and resistance, but also having direct effects on the risks and prevalence of damage. For example, high

temperature and prolonged drought may induce physiological stress in trees and at the same time are favorable to the development of pest insects, which can increase the number of generations (voltinism) and the rate of population growth. The same microclimatic conditions are known also to increase the frequency and severity of fires. Cool and wet conditions are often beneficial to fungal pathogens and of course more frequent strong winds increase the risk of storm damage. The selection of the site is the prominent decision that will determine in which climatic conditions trees, and associated antagonistic species, will develop, but other stand management options can also modify forest microclimate. In particular the selection of species (stand composition), the management of understorey cover, trough cleaning and regeneration practices, and the density of trees which results from thinning and harvesting regimes are main drivers of forest stand temperature, humidity and wind speeds.

The third main process which drives stand vulnerability and is affected by silviculture is *the provision of fuel and resources* to biotic and abiotic hazards. Even though trees are long living species, they are often not always suitable for herbivore pests and pathogenic fungi due to seasonal and yearly variations in accessibility or palatability. Pest and pathogen species therefore depend on alternative breeding substrates, or complementary food resources, to survive, such as other canopy or understorey plant species, slash, brush or remaining stumps. Moreover woody debris or understorey vegetation can fuel forest fires and therefore have an impact on canopy trees. Every silvicultural operation that can reduce such pest and pathogens reservoirs or limit the amount of alternate food and supplementary fuel would then decrease stand vulnerability to fire and biotic risks. For example the availability of alternate host plants for pest herbivores or pathogens greatly depends on site selection and preparation, stand composition and cleaning. The abundance of breeding substrates for insect and fungi such as stumps and slash are highly dependant on the frequency and intensity of thinning, pruning and harvesting. The type of regeneration will also affect the continuity of the forest cover and thus the permanence of suitable feeding or breeding substrates. By extension, if forms of shelter are viewed as self-protection resources, silvicultural operations which decrease the number of hiding sites for mammal herbivores (dense understorey) or refuges for insects and pathogenic fungi (logging or thinning residues) will decrease the associated risk of damage. The amount of fuel for forest fires mainly depends on the effectiveness of residue removal through adapted decisions about site preparation, cleaning, thinning, pruning and harvesting options. Conversely, changing stand composition may represent an effective way of limiting the accessibility of food resources to pests and pathogens, with non-host tree species developing physical or chemical barriers to host tree selection and colonisation.

The fourth main process only accounts for biotic hazards as it deals with maintenance or enhancement of *biological control by the natural enemies*. In many cases, forest pest and pathogen outbreaks are prevented or reduced in intensity by the impact of predators (mammals, birds or insects), insect parasitoids or antagonistic fungi. These biocontrol agents have similar life requirements than their host or their prey, e.g. supplementary or complementary food or breeding substrate to persist on site, shelters from adverse climatic conditions or enemies (super-predators). As a consequence, natural enemies may be affected by the same silvicultural operations as their target species of pest insect or pathogenic fungi. Control is optimised when for a given silvicultural operation the choice of an option results in a reduction in numbers of a particular pest and an increase in its natural enemies. A good example of this complementarity is provided by the effects of stand composition. Associations of certain tree species can reduce the accessibility of herbivorous insects to their host trees, while providing complementary habitats and resources for their predators. The decision making process is more difficult for the forest manager when a silvicultural practice leads to contradictory effects. For example changing site preparation, cleaning, thinning, pruning or harvesting practices with the aim of reducing the woody debris that are used for shelter, or as a breeding substrate, by pests and pathogens, can also reduce the abundance of microhabitats for their natural enemies. Resolving such contradictions will obviously require management compromises. An overview of how the four main processes influence the effects of silvicultural operations on forest stand vulnerability is shown in Table 1.

Table 1 Ranking of the relative relevance of the four processes driving the effect of eight silvicultural operations on forest stand vulnerability to mammal and insect herbivores, pathogenic fungi, fire and strong wind impacts. (0 – no, 1 – low, 2 – medium, 3 – high relevance)

	Tree physiology and development	Stand microclimate	Provision of food, fuel and shelters	Maintenance of natural enemies	<i>total</i>
Site selection	3	3	2	1	9
Site preparation	2	1	2	1	6
Stand composition	2	2	3	3	10
Genetic material	3	0	0	1	4
Type of regeneration	3	2	2	1	8
Cleaning	1	2	3	3	9
Thinning, pruning	3	3	3	2	11
Harvesting	1	2	2	2	7
<i>total</i>	18	15	17	14	64

Although only based on the mean scores from a survey of the opinions of the fourteen authors of this review, the simultaneous ranking of silvicultural operations and related ecological processes in relation to their effect on forest stand vulnerability gives new insight into the options for forest managers in minimising damage. It appears that the four processes driving stand vulnerability are of approximately equal importance. In contrast, the two silvicultural operations that have the greatest influence on stand vulnerability, i.e. stand composition and thinnings or pruning, indicate that

canopy structure and composition are of prominent importance. To a lower extent, site selection, site preparation and cleaning, which all relate to understorey management, have a strong effect on stand vulnerability. Lastly, the diversity of genetic material is considered be a weaker determinant of forest susceptibility to biotic and particularly abiotic hazards.

Conclusions

Silvicultural operations have multiple, sometimes contradictory, effects on stand vulnerability to various biotic and abiotic hazards. Forest management is therefore above all a question of compromises, where one has to balance risks and benefits not only for every single silvicultural operation but also for their possible interactions or cascading effects. Given the limited set of options that are at managers' disposal, it may be almost impossible at the stand level to find the correct balance. One way to circumvent these difficulties while keeping forest multifunctionality in perspective, would be to consider management at a larger scale, i.e. at the landscape level where it is possible to spread the risk by combining stands with different composition and management, such as intensively managed stands interspersed with natural forest remnants.

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