Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation

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Summary

Plant interactions can be defined as the ways plants act upon the growth, fitness, survival and reproduction of other plants, largely by modifying their environment. These interactions can be positive (facilitation) or negative (competition or exploitation). During plantation establishment or natural forest regeneration after a disturbance, high light levels and, sometimes, increased availability of water and nutrients favour the development of opportunistic, fast-growing herbaceous and woody species which capture resources at the expense of crop trees. As a consequence, the growth and survival of crop trees can be dramatically reduced. Although the effects of this competition are well documented, the physical and physiological mechanisms of competition are not. Moreover, the competition process is never constant in time or space. We present a conceptual competition model based on plant growth forms common in global forests, i.e. graminoids, forbs, small shrubs, large shrubs and mid-storey trees, and main-storey trees. Their competitive attributes and successional dynamics are examined. An overview is presented on the way forest vegetation management (FVM) treatments influence these components and outcomes regarding crop tree performance and diversity conservation. Finally, a synthesis of literature yields FVM guidelines for efficiently optimizing crop tree performance and safeguarding diversity. Future research needs to further sustainable FVM are presented.

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Introduction

Competition between trees and natural vegetation in newly established plantations and naturally regenerated forests is the major process influencing tree establishment and growth, and drives succession (Bazzaz, 1990; Thompson and Pitt, 2003). Evidence of the benefits of vegetation control for enhanced tree growth is widespread (Wagner *et al.*, 2005), yet there is still a lack of general principles for forest vegetation management (FVM) regarding the strategies to apply to optimize desired tree survival and growth, while conserving floristic diversity. This review will summarize FVM research to lead us to a formulation of general FVM strategies for sustainable forest regeneration and management.

Plants interact by many different mechanisms, including beneficial or detrimental climatic modifications, resource addition or depletion, allelopathic chemical release, and alterations in herbivore, pathogen or mycorrhizae abundance (Tilman, 1988; Grace and Tilman, 1990; Anderson and Sinclair, 1993). Literature on the effects of vegetation on crop seedling survival and growth shows that competition varies greatly depending on crop tree species (Fredericksen *et al.*, 1993; Wagner *et al.*, 1996; Zutter *et al.*, 1997; Mitchell *et al.*, 1999; Kuessner *et al.*, 2000; Reynolds *et al.*, 2002a, b), seedling size (South *et al.*, 1995, 1999; Rose and Ketchum, 2003), vegetation composition (Cain, 1999; Coll *et al.*, 2003; Miller *et al.*, 2003a), site characteristics (Lautenschlager, 1999; Powers and Reynolds, 1999) and silvicultural treatment (Gemmel *et al.*, 1996; Haywood *et al.*, 1997). Wagner *et al.* (1999) also pointed out that competitive interaction between seedlings and surrounding vegetation is a dynamic process with strong temporal variations over the first years after seedling establishment, which are determined by the pattern of seedling and vegetation development (Miller *et al.*, 2003a, b).

The large body of global literature examining the competitive effects of surrounding vegetation on tree seedling development covers a wide range of plant and tree species, site conditions and silvicultural contexts. This synthesis is based on the concept that it is possible to reduce this complexity by grouping plant species into a limited number of types, principally determined by growth form as well as taxonomy, life history, morphological and/or physiological plant traits as proposed by Goldberg (1996). The concept of plant functional type has concerned community ecologists for decades (Grime, 1979; Gitay and Noble, 1997; Lavorel and Garnier, 2002) and the relationship between plant traits and competitive ability has received much attention. However, most of the existing studies on these relationships were performed in plant communities other than forests, such as wetlands, grasslands or pastures (Goldberg, 1996; Rösch *et al.*, 1997; Dietz *et al.*, 1998; Wardle *et al.*, 1998), while we will focus this review on vegetative competition in forest plantations and naturally regenerated stands.

The specific objectives of this review are:

1. to identify the main mechanisms of resource competition among plants, and analyse the relationships between various plant traits and competitive ability.
2. to define a limited number of groups of species with similar competitive ability towards tree seedlings based on experimental data and the existing literature. Species will be grouped according to their competitive magnitude and the temporal pattern of the competitive effects on crop tree growth and survival. Each group will be characterized by a series of plant traits known to be related to competitive ability under specific environmental conditions.
3. to assess the effects of the main silvicultural treatments applied in young forest stands (e.g. herbicide applications, mechanical treatments and shelterwood cuts) on the composition and the development of the different species in the groups defined earlier, and the consequences on the competitive effects of the surrounding vegetation.
4. from all this review and knowledge, to examine the practical consequences for sustainable FVM as well as the needs for future research.

General mechanisms of resource competition among plants

Resource competition occurs when plant individuals utilize the same pool of growth-limiting resources. All plants require light, water and inorganic nutrients, and the combined demand of plant individuals for a resource may exceed the immediate supply, leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals (Begon *et al.*, 1990).

The ability of individual plants to compete is related to the efficiency to which they acquire and use resources, which in forestry is highly related to their hierarchy within a forest stand. There are two ways in which individual plants can effectively compete: by rapidly depleting resources to a low level and/or being able to survive and grow at lower resource levels (Goldberg, 1990). The relative importance of the two processes for the outcome of competition between plant individuals strongly depends on the level of resource availability. In high resource environments, species with high relative growth rates are effective competitors because rapid growth enables them to dominate available space and to acquire the most resources (Grime, 2001). In low resource environments, traits that lead to resource retention are far more important for plant performance than traits that lead to a high ability for resource uptake (Aerts, 1999). Because there is a fundamental trade-off between the traits allowing maximization of resource acquisition through rapid growth and the traits allowing resource conservation through reductions in tissue turnover, there is no superior competitor that out competes all other species in all environments, but rather a series of competitive strategies adapted to specific environments (Lambers *et al.*, 1998).

Traits associated with competition for nutrients and water

Numerous studies have shown that in fertile environments, species maximizing nutrient acquisition compete most effectively. The rate of nutrient acquisition by a plant is a function of the rate of uptake per gram of biomass, its total biomass, and the proportion of biomass allocated to the nutrient-absorbing roots. Enzymatic kinetics of nutrient uptake by roots are an important determinant of the uptake of mobile elements such as nitrogen, whereas the uptake of immobile ions such as phosphate primarily depends on morphological traits (Casper and Jackson, 1997; Aerts and Chapin, 2000) and the less understood mycorrhizae associations (Allen and Allen, 1990; Sands and Mulligan, 1990).

Plant performance is determined not only by the amount of nutrients absorbed, but also by the amount of nutrients lost. Nutrient losses may occur through tissue turnover, herbivory, leaf leaching and root exudation. Most nutrients that are lost cannot simply be taken up again by the same plant, but in order to maintain biomass, a plant needs to replace the same quantity of nutrients that it has lost (Berendse and Elberse, 1990). In infertile habitats where nutrient acquisition is a costly process, successful competitors are characterized by numerous features that reduce nutrient losses, such as long tissue lifespan and low nutrient concentration in senesced tissues (Aerts, 1999) due to an efficient retranslocation prior to abscission (Vitousek, 1982; Nambiar and Fife, 1991).

On sites with high water availability, successful competitors are characterized by a high growth rate, associated with a maximization of stomatal conductance and water loss. On water-limited sites, plant performance and competitive ability are related to morphological and physiological traits designed to reduce water loss and increase water use efficiency (low stomatal conductance, low stem hydraulic conductivity, and low transpiring surface area through adapted leaf morphology). Some features such as early leaf abscission during drought conditions characterize tree strategies to reduce moisture loss that also influences photosynthetic rates, while mycorrhiza symbionts may also assist in water uptake on dry sites and require shared photosynthates (Sands and Mulligan, 1990).

In forests, nutrient and water availability exhibits high spatial and temporal heterogeneity, to which plants must adjust (Nobel, 1994; Stark, 1994). Important vertical gradients in both nutrient and water availability exist, with nutrients generally largely concentrated in the upper soil layer, whereas water availability generally increases with depth (Sands and Mulligan, 1990). Significant variations in nutrient concentration occur at scales relevant to individual plants, with the existence of highly localized zones of high nutrient availability, resulting from the activity of plants, animals and microorganisms. Furthermore, nutrient concentration and water content usually exhibit large seasonal fluctuations. In spatially or temporally variable environments, rapid adjustments in morphology and physiology in response to highly localized and temporally transient zones of high nutrient or water availability allow a species to maintain dominance over other competing species, by facilitating its resource acquisition from nutrient-rich or moist patches (Caldwell, 1994; Fitter, 1994).

Traits associated with competition for light

Young trees may grow under contrasted light conditions, from full sunlight for seedlings planted after a clearcut to very low light levels for naturally regenerated seedlings occurring under a dense shelterwood. In high light environments, competitive ability is related to a suite of morphological and physiological traits, allowing the plant to expand rapidly its leaf area above its neighbours through high leaf nitrogen content, high photosynthetic and dark respiration rates, high growth rate, high leaf and root turnover, high allocation to stem growth, and long shoots and petioles (Bazzaz, 1996).

In low light environments, fast-growing species usually have low survival rates and do not compete effectively. Successful competitors are characterized by their ability to survive in shaded understorey and to respond effectively to canopy openings (Messier *et al.*, 1999). Ability to survive in understorey environments is linked to the maintenance of a positive carbon budget, allowed by the optimization of light capture in shade (thin leaves, high efficiency to respond to sunflecks, crown architecture designed to reduce self-shading and to maximize the capture of diffuse light) and by the maintenance of low respiration rates, low leaf photosynthetic capacity, long tissue life-span and low total biomass (Kozlowski *et al.*, 1991).

Spatial and temporal segregation

Competition occurs when plant individuals prospect the same volume of above- or below-ground space at the same time. Spatial and temporal segregation of roots and shoots by neighbouring plants may be a means of reducing competition and hence species that forage different zones, or species that take up resource at different periods, may coexist without competing. This is the reason why in agroforestry systems (Schroth, 1995), and to a much lesser extent in forestry, plants having different spatial and temporal development patterns are chosen as a priority to avoid or at least decrease competition between plants and hence optimize their growth.

Initially roots of competitors and tree seedlings equally occupy the same soil horizons (Zutter *et al.*, 1999; Balandier *et al.*, 2002). Vertical stratification of root systems is an eventual pattern observed in many habitats, with shallow-rooted herbaceous species utilizing shallower resources and deep-rooted woody plants acquiring separate resource from deeper soil horizons (Nambiar and Sands, 1993; Casper and Jackson, 1997). When grown in isolation, both herbaceous and woody species have their roots concentrated in the topsoil. For vertical stratification to happen when grown in competition, a shift in the vertical root distribution of at least one species has to occur, and only species with plastic root systems are able to reduce root competition from neighbouring species by adjusting their root distribution (Zutter *et al.*, 1999).

However, even with a vertical stratification of root systems, the plant that has roots in the deepest horizon can suffer from the plant colonizing the upper horizon as a consequence of an almost complete withdrawal of soil water coming from rainfall by the roots in the upper soil layer and the gradual drying of the deeper soil layers. Hence, the filling of all the soil layers with water in spring is fundamental for both plant types (Balandier, unpublished data).

Similarly, temporal differences in resource use facilitate species coexistence, and species with different seasonal phenologies may reduce the intensity of competition (Kimberley and Richardson, 2004). Differences may range from a complete separation when one species grows after the other has died, to differences in the timing of maximal resource uptake (Schroth, 1999).

Competitive effects of different plant species groups on tree seedlings

The different species commonly found in forest stands at different stages can be separated into five large groups: graminoids (including Poaceae, Cyperaceae and Juncaceae), forbs (herbaceous dicots), small shrubs (including semi-woody plants and ferns), large shrubs and mid-storey trees, and main-storey trees. We hypothesize that plant species within a group can be considered to follow similar temporal patterns of competitiveness against crop trees. The competitive pattern describes the main resource for which the plants compete with the crop trees, the survival and growth response of the crop trees, and the time-course of the competitive effects in the years following stand establishment. For each of the five groups, the competitive pattern and the main plant traits associated with the pattern will be described. These features are summarized in Table 1 (Frochot *et al.*, 2002). This does not mean that a plant within a certain growth-form group is always a predictable competitor, but rather that it could be a competitor in some contexts and must be considered with care as far as crop tree growth and vigour are concerned.

Graminoid species vary tremendously in their growth rates, ability to form continuous canopies, below-ground root density, and stature. Sparse, low-growing grasses may have little influence on crop tree growth, while dense fields of tall grass can completely exclude crop tree survival (Kozlowski, 2002). The detrimental effects of perennial grasses such as *Andropogon* sp., *Calamagrostis* sp., *Dechampsia* sp., *Imperata* sp. and *Molinia* sp. on tree seedling establishment has been widely reported and they are perhaps the most widely recognized competitors of tree seedlings (Davies, 1987; Otsamo *et al.*, 1997; Mitchell *et al.*, 1999). They generally have a very dense root system, made up of a very high number of thin roots (Ludovici and Morris, 1997; Zutter *et al.*, 1999; Balandier, unpublished data). Their specific root length (i.e. the root length by unit of root weight, which can be considered as the possibility of exploring soil volume for a given investment in carbon) can reach 200–700 m g DW^{-1} (Zutter *et al.*, 1999*;* Atkinson, 2000) while that of some tree species such as *Fagus sylvatica* or *Pinus sylvestris* is often limited to 10–35 m g^{-1} (Curt *et al.*, 2005). This feature allows graminoids to colonize efficiently new soil volume and to take up rapidly available resources. Grasses have a shallow root system with maximum root depth being much less than 1 m for most grass species (Kutschera and Lichtenegger, 1982). The root system of the newly established tree seedlings is localized in the same soil horizons as the grass roots. The grass root system constitutes a physical barrier that strongly restricts the growth and resource uptake of seedling roots. The competitive effect of the grasses may be extremely high in the first years after seedling establishment but, if the seedling survives, it progressively develops its root system in deeper soil horizons and escapes grass root competition. Grass root competition usually causes high seedling mortality following planting, but its effects on seedling growth are often restricted to a few years after planting (Miller *et al.*, 2003b; Figure 1).

The dense and shallow root system of grasses strongly reduces the penetration of rainfall into the soil but usually does not withdraw any water from horizons deeper than 1 m (Balandier, unpublished data). On soils where water is available in deeper horizons that can be reached by the tree roots, the competitive effects of the grass are limited. By contrast, on shallow soils or on soil with no deep water-table, rainwater is the major source of water and the presence of a dense grass layer that pre-empts most of this water has a highly negative impact on tree seedlings.

Grasses differ considerably in their ecological strategies: some species which are specific to fertile and well-drained sites, such as *Agrostis* sp. or *Calamagrostis* sp., show high growth rate, high nutrient uptake capacity and high physiological and morphological plasticity (Grime, 1994; Collet *et al.*, 1996). These species are able to very rapidly colonize the stand following partial or clearcutting and, because of their ability to deplete rapidly available soil resources, are very competitive towards tree seedlings (Picon-Cochard *et al.*, 2001; Hangs *et al.*, 2003; Coll *et al.*, 2004). Other grass species that are more specific to infertile, dry or waterlogged sites, such as *Deschampsia cespitosa* or *Molinia* sp. show low growth rate and slow tissue turnover (Aerts and Chapin, 2000). These species are generally not as efficient in colonizing newly opened stands even if, in certain circumstances, *Deschampsia* can also rapidly respond to increased light after cutting. However, once they are installed, they are able to prevent the establishment of almost any new species, because of their ability to grow effectively under resource-limited conditions (Coll *et al.*, 2003; Figure 2).

As erectophiles (leaf angle ≥65°) with clumped foliage, grasses generally do not intercept a great amount of light in comparison with other species

Table 1: Main traits conferring competitive ability and potential effects on the crop tree of different groups of plants according to their growth form (modified from Frochot *et al.*, 2002 by kind permission of the author)

Growth form	Example of genus	Main traits	Main possible effects	Main references
Graminoids (and mainly social perennial grasses)	*Agropyron* *Agrostis* *Andropogon* *Brachypodium* *Calamagrostis* *Deschampsia* *Digitaria* *Holcus* *Molinia* *Panicum*	Dense root system with high physiological ability to uptake water and nutrients High growth rate	Competition for water, nutrients and soil space	Adams *et al.*, 2003 Balandier *et al.*, 2005 Coll *et al.*, 2003, 2004 Frochot *et al.*, 2002 Hangs *et al.*, 2002, 2003 Ludovici and Morris, 1997 Mitchell *et al.*, 1999 Mohammed *et al.*, 1998 Morris *et al.*, 1993 Picon-Cochard *et al.*, 2001 Reynolds *et al.*, 1998, 2002a, b Schütz, 2004
Forbs with a dense cover	*Chenopodium* *Conyza* *Epilobium* *Rumex* *Trifolium*	High aerial growth rate Dense cover	Competition for light, in some situations also for water and nutrients	Davies, 1987 Frochot *et al.*, 2002 Hangs *et al.*, 2002, 2003 Hänninen *et al.*, 1999 Löf, 2000 Sands and Nambiar, 1984 Schütz, 2004
Small shrubs with a dense cover	*Cytisus* *Genista* *Rubus* *Sesbania*	High aerial growth rate Dense cover	Competition for light, in some situations also for water and nutrients	Carrère *et al.*, 2003 Fotelli *et al.*, 2001, 2002 Frochot *et al.*, 2002 Morris *et al.*, 1993 Schütz, 2004 Watt *et al.*, 2003
Tall shrubs and mid-storey trees	*Alnus* *Betula* *Carpinus* *Populus* *Salix*	Can overtop crop tree	Competition for light, in some situations also for water and nutrients	Balandier *et al.*, 2004 Cain, 1997 Frochot *et al.*, 2002 Jobidon, 2000 Reynolds *et al.*, 1998, 2002a, b Rose *et al.*, 1999 Schütz, 2004
Main storey trees	*Acer* *Carya* *Liquidambar* *Pinus* *Prunus* *Quercus*	Can overtop crop tree and be codominant in final stand	Competition for light, water, nutrients, and space	Albaugh *et al.*, 2003 Fredericksen *et al.*, 1993 Glover and Zutter, 1993 Glover and Quicke, 1999 Mitchell *et al.*, 1999

groups (Reynolds *et al.*, 2002a; Sonohat *et al.*, 2002; Figure 3). In the southern US, dense stands of two common early competitive grasses of *Pinus taeda* L., *Panicum dichotomiflorum* and *Andropogon virginicus*, both significantly decreased soil moisture but not light in the first 2 years after planting (Morris *et al.*, 1993). Mitchell *et al.* (1999) studied *Pinus taeda* growth responses to gradients in the density of the tree *Liquidambar styraciflua* and the grass *Andropogon virginicus*. *Liquidambar* affected *Pinus* growth mainly by reducing light availability while *Andropogon* reduced pine growth mainly by decreasing soil water content. At the end of the first growing season, four *Andropogon* plants per square metre reduced *Pinus* stem volume

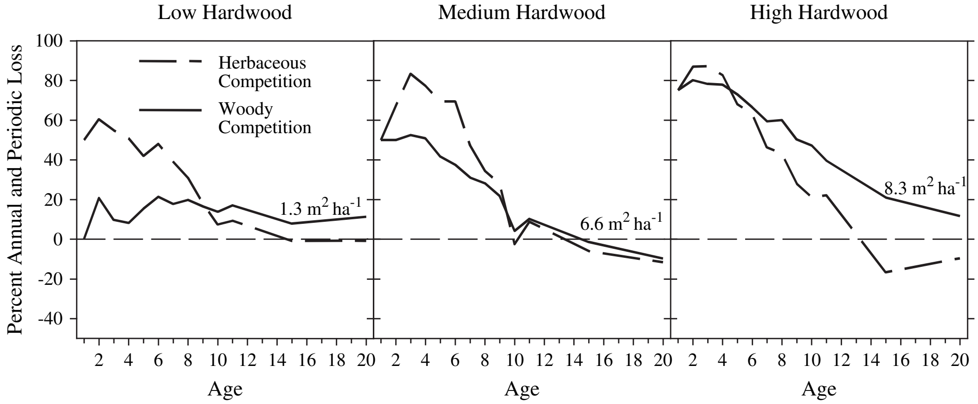

Figure 1. Duration and intensity of herbaceous *vs* woody competition in *Pinus taeda* plantations in the south-eastern United States. The annual (years 1–11) and periodic (years 11–15 and 15–20) loss in loblolly pine (*Pinus taeda*) growth (percentage loss relative to total vegetation control per year or period) from woody competition only (hardwoods mainly and shrubs) and herbaceous competition only at three study locations differing by their hardwood density (Miller *et al.*, 2003b, and Miller, unpublished 20-year data). Values for the hardwood basal area at year 20 are provided on the figure. During the first years following pine plantation, herbaceous competition is predominant, particularly when the standing volume of hardwood is low. Conversely, some years after, competition by woody species become higher than that of herbaceous species. Both decrease with time and the competition effect is close to zero at about age 15–20 years.

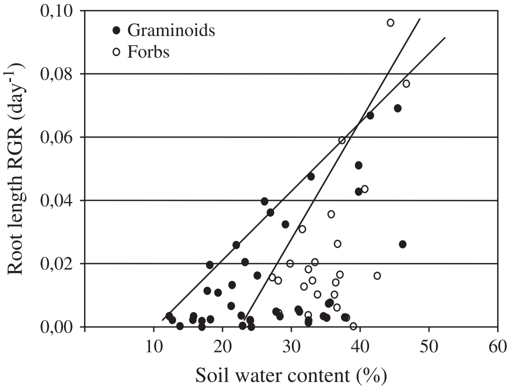

Figure 2. Root growth ability according to soil water content for two plant groups, graminoids and forbs. Root length relative growth rates (RGR) were computed from weekly measurements of root growth through rhizotrons during the growing season in 2001. Soil water content in the 0–20 cm soil layer was measured at the same time with a TDR probe in a close vicinity of each rhizotron. (Data from central France, adapted from Coll *et al.*, 2003 by kind permission of the author) The lines give the maximum growth for the two groups of plants. Obviously graminoid roots are able to grow better at low soil water content than forb roots.

index by 60 per cent, while increasing *Andropogon* density to 16 plants per square metre only reduced pine stem volume index by an additional 22 per cent. Even low densities of bunch grasses in droughty conditions present severe competition to tree seedlings.

Herbaceous forbs can be less competitive than graminoids, at least for soil resources (Coll *et al.*, 2003; Figure 2). Their root growth is slower than grass species, especially during increasing soil drought. This limits the forb's capacity to explore new soil volumes and reach patches with high water or nutrient availability, in comparison with grasses. Therefore forbs generally present a sparse cover in a resource-limited environment (Miller *et al.*, 1995; Lautenschlager, 1999). In fertile sites, they can compete efficiently for nutrients as shown by Hangs *et al.* (2003) for *Epilobium angustifolium* and Morris *et al.* (1993) for forb mixtures. However, light is the resource for which forbs compete the most efficiently (Frochot *et al.*, 2002). The leaf area index (LAI) of species such as *Epilobium angustifolium* can reach 3.4 (Kuessner *et al.*, 1998; Table 2). Morris *et al.* (1993) found that *Pinus taeda* seedlings experienced less competition for soil moisture and

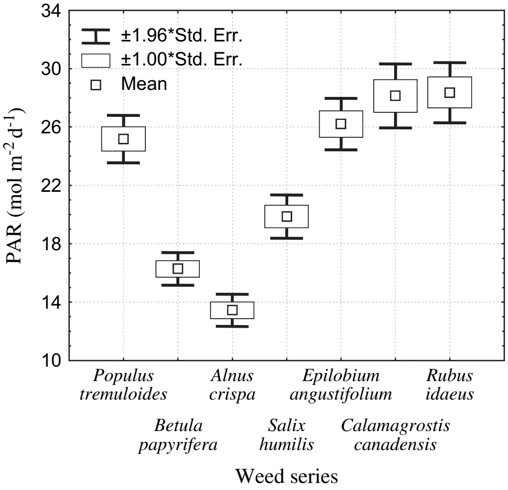

Figure 3. Effects of seven important boreal weed species on *Picea mariana* mid-crown photosynthetically active radiation (PAR) seasonal availability. Data are given as mean (± standard error) of three soil types (clay, loam and sand soils) six growing seasons after planting in Ontario, Canada (Reynolds *et al*., 2002a). Weed species were cultivated as monospecific culture in small plots with different controlled densities. Tree competitors (*Salix*, *Alnus*, *Betula* and to a lesser extent *Populus*) generally overtopped spruce 6 years after plantation and, hence, decreased more PAR availability for spruce than herbaceous species, resulting in reduced spruce seedling growth.

nutrients from a dense mixture of forbs compared with *Panicum dichotomiflorum* and *Andropogon virginicus* grasses, on one hand, or *Sesbania exaltata* subshrub, on the other hand. By contrast, forbs decreased light more than these in the second year. All in all, seedling growth was higher with forbs than with grasses or small shrubs.

Small shrubs such as those of the genera *Rubus*, *Genista* and *Sesbania* are often much more problematic. These species usually develop a root system not as dense as the grass root systems, but much deeper (Kutschera and Lichtenegger, 1992). They can take up significant amounts of water and nutrients from soils (Morris *et al*., 1993; Thevathasan *et al*., 2000; Fotelli *et al*., 2001, 2002; Reynolds, 2002b), and thus reducing seedling growth. Their most dramatic effect on tree seedlings is the reduction of available light. They develop a medium-sized stature (up to 2 m in some cases) that may rapidly overtop the seedlings. The LAI of species such as *Rubus idaeus* may be as high as 2.8 (Kuessner *et al*., 1998; Table 2), and the relative light intensity under the shrub canopy may be as low as 5 per cent of full light intensity (Kuessner *et al*., 2000). The LAI for the legume *Sesbania exaltata* can reach 4.2 in 1 year and presented strong competition for water and nutrients as well as light, comparable to grasses (Morris *et al*., 1993).

In the early post-harvest years when small shrubs can completely overtop seedlings, they usually induce high seedling mortality. For instance, in natural regeneration of *Quercus petraea* and *Q. robur* stands, the presence of a 50-cm-high continuous layer of *Rubus fruticosus* may totally suppress the new *Quercus* seedlings (Frochot *et al*., 2002). In two sites in northern Europe, reduction of shading from *Pteridium aquilinum* resulted in increased growth of *Fagus sylvatica* and *Pinus sylvestris* seedlings while the role of below-ground competition was negligible (Den Ouden, 2000). This can be due to the low amount of roots attached to bracken rhizomes. The detrimental effects of small shrubs and tall ferns (such as *Pteridium aquilinum*) are limited to a few years after seedling establishment and, if the seedlings are able to survive the strong competitive effects of the deciduous small shrubs, they will eventually reach the top of the shrub canopy and progressively escape their competitive effect while others will not, due to light requirements (Horsley, 1993; Reynolds *et al*., 2002a).

The competitive effects of tall shrubs and mid-storey trees vary strongly according to their origin (seedlings or sprouts), abundance and phenology (evergreen or deciduous). Severe competition by tall evergreen shrubs is common in the coastal plain forests of the southern US and boreal forests of Canada. In the north-western forests of the US, shrub competition is highly variable from slight to severe (Harrington *et al*., 1995; Rose *et al*., 1999). Their main competitive ability is via light interception (Kuessner *et al*., 1998, 2000; Jobidon, 2000; Reynolds *et al*., 2002a, b; Figure 3 and Table 2). The competitiveness of these species depends primarily on the dynamics of their development and the rate at which they may overtop the seedlings. Many of the broadleaved species are capable of sprouting vigorously from stumps

Table 2: Mean LAIs ($m^2 m^{-2}$) of seven important boreal competing species, fourth growing season (1997) in Ontario, Canada (adapted from Kuessner *et al.*, 1998 by kind permission of the author)

	Clay site			Loam site		
Competitor	Mean	SD	*n*	Mean	SD	*n*
Alnus crispa	1.98	± 0.89	27	0.79	± 0.38	27
Betula papyrifera	1.96	± 0.57	27	0.78	± 0.52	27
Populus tremuloides	0.97	± 0.57	37	0.53	± 0.28	26
Salix humilis	1.57	± 0.60	31	0.72	± 0.28	27
Calamagrostis canadensis	1.06	± 0.71	32	1.04	± 0.45	27
Epilobium angustifolium	3.44	± 0.82	27	1.01	± 0.41	27
Rubus idaeus	2.81	± 1.25	27	0.58	± 0.49	27

or established rootstocks producing rapidly growing sprouts that quickly overtop the slower growing seedlings. Other species, such as *Betula papyrifera*, *Populus tremuloides*, *Ilex glabra*, *Cytisus scoparius* and *Buddleja davidii*, produce an abundant seed crop that can quickly invade open sites and are capable of rapid juvenile growth. Whatever the origin of the competing broadleaves (sprout or seed), they are capable of dominating the site for many years and can greatly reduce crop tree stocking and growth (Zutter and Miller, 1998; Richardson *et al.*, 1999).

Tree species of main-storey stature are severe competitors of young trees in many forest regions, especially those from sprout origin (Glover and Zutter, 1993; Wagner *et al.*, 2005). Within a region, main-storey tree abundance can vary widely, unlike the more ubiquitous grass and forb competitor components. The competitive effects can occur early in stand establishment following abundant resprouting, and are comparable to herbaceous competitors in magnitude (Miller *et al.*, 2003a; Figure 1). With main-storey tree species, the competitive effects persist the longest of all competitive groups, especially when tree competitors are dominant or co-dominant with the desired trees (Shainsky and Radosevitch, 1991; Glover and Zutter, 1993; Glover and Quicke, 1999, Reynolds *et al.*, 2000a, b). In some world forests, non-sprouting, fast-growing conifers also can form dense early stands to compete with regeneration, which can even be the same species as crop trees, although not genetically improved. Volunteer *Pinus taeda* commonly compete with planted improved seedlings in the southern US along with other pines species, *Pinus echinata* and *P. virginiana* (Miller *et al.*, 2003a).

Main-storey tree competitors have been shown in both boreal and temperate forests to exert severe competition even at low densities. In the boreal forests of Canada studies showed that *Rubus idaeus* or *Calamagrostis canadensis* exerted a strong competition, particularly for nutrients in the first years after plantation, but by year 6, available light, soil temperatures and soil moisture were reduced most by arborescent competitors (*Alnus crispa*, *Betula papyrifera*) that generally overtopped *Picea mariana* seedlings (Reynolds *et al.*, 2002a; Figure 3).

These findings for major boreal weed competitors are consistent with those reported by other researchers carrying out similar density studies with major temperate weed competitors in the US. Glover and Quicke (1999), working with two arborescent competitors, *Liquidambar styraciflua* and *Quercus nigra*, planted in a gradient of densities in *Pinus taeda* plantation, reported that both competitors greatly reduced pine growth at the lowest weed densities, but had progressively less additional effect as weed density increased. Using a designed experiment established by Mitchell *et al.* (1993), Perry *et al.* (1993) studied *Pinus taeda* growth responses to gradients in *Liquidambar styraciflua* and *Andropogon virginicus* density during the first year of *Pinus* growth. *Liquidambar* densities as low as one plant per square metre signficantly reduced *Pinus* growth as early as May during the first growing season. A density of one sprout per square metre of *Liquidambar* resulted in a 75 per cent reduction in *Pinus* stem volume index. Adding an additional one or three sprouts per square metre only reduced *Pinus* growth by an additional 4 or 16 per cent, respectively. *Liquidambar* sprouts resulted in more growth loss than established *Andropogon*. Shainsky and Radosevich (1991) worked with mixtures of *Pseudotsuga menziessi* and *Alnus rubra* planted at differing densities and at the same time. During the third year, the lowest density of *Alnus* (1 plant m^{-2}) inflicted a substantial reduction in *Pseudotsuga* stem volume, with progressively less additional growth reduction as *Alnus* density increased.

In some circumstances crop trees can tolerate this competition and become dominant and the harmful effect of competitors can lessen (Miller *et al.*, 2003a; Figure 1). Depending on the objectives of the forester, this situation can be a good compromise, non-crop trees being not too deleterious for crop tree growth, while adding diversity to the stand and preventing competition by shading the plants of the other groups of competitors like grasses, forbs and small shrubs (Wagner *et al.*, 1999). The magnitude of these competitive reductions, especially by mid-storey and overstorey hardwoods, depends on the shade tolerance of the crop tree. Some crop trees such as *Fagus sylvatica*, *Acer pseudoplatanus* or *Abies alba* in Europe are tolerant enough to survive and grow in the understorey of the competing trees for decades and will eventually reach the overstorey and achieve dominance. Other crop trees such as *Quercus petraea*, *Q. robur*, *Q. rubrum*, *Prunus avium* and *P. serotina*, which are shade intolerant, are not able to survive in the understorey and are rapidly suppressed by the competing hardwoods (Marquis, 1990).

Like the species from the other groups, the tall shrubs and trees may have both detrimental and beneficial effects on seedling development (e.g. Frochot *et al.*, 2002; Schütz, 2004). However, the beneficial effects of tall shrubs and trees (mainly obtaining a straight stem free of knots by natural pruning) are of primary importance for some crop trees such as *Quercus petraea* and *Fagus sylvatica*. The sale price of wood of high quality intended for furniture in Europe can be more than fivefold higher than wood for carpentry for species like *Prunus avium*, *Fraxinus excelsior*, *Acer pseudoplatanus* and *Quercus rubra* (Ancel, 1995), justifying a crop tree growth reduction for a better stem quality provided by the shelter created by other trees and tall shrubs. Positive (better stem quality) and negative (growth reduction) effects are intrinsically correlated (Balandier *et al.*, 2004), being both the consequence of the light availability reduction caused by the neighbouring species, and it is therefore difficult to disentangle them (Collet *et al.*, 1998). The relative importance of detrimental and beneficial effects depends on site conditions, vegetation composition, and the stage reached by the crop trees (Cain, 1997; Jobidon, 2000; Frochot *et al.*, 2002).

Short-term effects of silvicultural treatments on vegetation dynamics

Determinants of vegetation dynamic

Whatever the vegetation management treatment or the silvicultural operation, vegetation is never at a complete equilibrium. The technical operations can be seen as more or less intense disturbances of the ecosystem that induce secondary plant succession with changes, both in plant cover and species composition. Therefore in order to design management strategies, it is necessary to predict for the various vegetation management options the changes in both plant cover and species composition, which usually leads to changes in the overall competitive effect of the vegetation. Unfortunately, successions and particularly vegetation composition and species dominance are not easy to predict. Succession is determined by initial floristic composition, the arrival of new species from adjacent areas (Haeussler and Bergeron, 2004), and the changes in the relative dominance and interactions among the different species. It is recognized that stochasticity plays a central role in all these processes (Egler, 1954) and it seems unrealistic to predict with accuracy vegetation composition and cover, species by species, resulting from a silvicultural intervention.

However, succession science indicates that it is possible to anticipate the vegetation changes in wide plant groups, as those defined in the previous section. Following a clearcut, pioneering plants with widely dispersed seeds such as grasses and some forbs that often reside in the soil seed bank characterize the first stage of succession, if resprouting woody plants are not present (Miller *et al.*, 1995). In some situations, a dense cover of monopolistic plants, such as a grass or invasive plant, can stop succession (Otsama *et al.*, 1997). The following stages are often characterized by the occurrence of small shrubs and later by pioneering small trees before the establishment of true forest trees (Connell and Slatyer, 1977; Perry, 1995; Rameau, 1999). These stages do not necessarily all occur in all situations. For example, after a clearcut, re-sprouts of shrubs or trees can directly lead to a shrubby stage, and pioneering trees (such as *Pinus sylvestris* and *Betula pendula*) can directly establish in meadows characterized by grass and annual forbs (Curt *et al*., 2003).

Taking into account this general plant succession pattern, we will describe in this section the short-term effects of various silvicultural operations on the vegetation dynamics, and analyse their consequences on the competitiveness of the vegetation against the crop trees.

Herbicide application and species replacement

Herbicides are commonly used to control vegetation competition in some forest regions (Reynolds, 1988; Campbell, 1990, 1991; Reynolds *et al*., 1993; Richardson, 1993; Wagner, 1993, 1994; Lautenschlager *et al*., 1998; Willoughby, 1999; Thompson and Pitt, 2003), with the objective being to eliminate or reduce growth of one, several or all herbaceous or woody plants competing with crop trees, in order to improve their establishment and growth. Herbicides are used for afforestation of former agricultural or grass lands as well as for reforestation of forest stands by planting or natural regeneration. At first, the herbicide leads to the suppression of the target species or at least to a strong reduction of their development. But this effect is usually only temporary and vegetation redevelops. The vegetation cover can reach between 0 per cent and 80 per cent at the end of the first year after the treatment, depending on site richness (Dreyfus, 1984; Zutter *et al*., 1986; Cain, 1999; Miller *et al*., 2003a) and residual activity of the herbicide. Vegetation composition can be partially or completely different from the initial one (Dreyfus, 1984; Pitt *et al*., 1988; Reynolds and Obarymskij, 1994; Willoughby and McDonalds, 1999) which may be less detrimental for crop trees (Pitt *et al*., 1988), but alternatively can also be more competitive than the initial vegetation (Horsley, 1988; Groninger *et al*., 2004). Several examples of such vegetation replacement are found in the literature (Dreyfus, 1984; Pitt *et al*., 1988; Dumas *et al*., 2000; Table 3). In practice, it is often difficult to

Table 3: Some examples of the evolution of the dominant vegetation after a herbicide treatment in different site conditions (from Dreyfus, 1984; Pitt *et al*., 1988; Dumas *et al*., 2000)

Soil	Chemical composition of herbicides	Initial dominant species	Dominant species after treatment
Waterlogged soil	Atrazine	*Agrostis* spp. *Juncus* spp.	*Deschampsia cespitosa* *Holcus lanatus* *Ranunculus repens* *Molinia caerulea*
Well-drained soil	Atrazine	*Agrostis* spp.	*Rubus fruticosus*
Rendzina	Hexazinone Dalapon + Dichlobenil	*Brachypodium pinnatum* *Carex flacca*	Herbaceous dicotyledons *Carex flacca* *Brachypodium pinnatum* *Clematis vitalba*
Granitic soil	Dalapon + Dichlobenil	*Deschampsia flexuosa* *Agrostis capillaris*	*Deschampsia flexuosa*
Granitic soil	Atrazine	*Cytisus scoparius*	*Agrostis capillaris* *Cytisus scoparius*
Acid and waterlogged soil	Asulame	*Pteridium aquilinum*	*Molinia caerulea* *Calluna vulgaris*
Acid soil	Asulame	*Pteridium aquilinum*	*Holcus lanatus* *Cytisus scoparius*
Clay	Hexazinone	*Rubus ideaus*	*Epilobium angustifolium*

predict the changes in vegetation following a herbicide treatment in different environments, even for a vegetation characterized by the same dominant species (or a group of the same dominant species) as it depends also on the ecological features of the site, phenological plant stage, application technique, eventual soil tillage before treatment and soil seedbank composition.

In some particular situations, a herbicide application may eventually lead to a more diversified flora by suppressing the dominant species (e.g. shrubs and trees) and freeing space and resources for the other species (e.g. diverse forbs) (Miller *et al.*, 2003a). However, in most cases, a new colonizing species becomes dominant in the following years leading again to heavy competitive effects on crop trees (Dumas *et al.*, 2000). Therefore in some cases, it can be necessary to continue herbicide applications for several years and often until canopy closure occurs and crop trees start to dominate and suppress weed growth (Willoughby and McDonald, 1999). However, it has been well substantiated by multiple studies that vegetation control in the initial 1–2 years after establishment yields the most crop tree response, a 'critical period' for control (Bacon and Zedaker, 1987; Newton and Preest, 1988; Lauer *et al.*, 1993; Glover and Lauer, 1996; Wagner *et al.*, 1999).

It is important to note that herbicide application has more impact on relative species dominance than species composition or species diversity (i.e. the species composition after a treatment is basically the same as in an untreated control, but it is not the same species that are dominant; Dreyfus, 1984). Such results were also reported by Boyd *et al.* (1995) and Miller *et al.* (1999) in central Georgia (USA) who observed in *Pinus taeda* plantations that 10 and 11 years after different single herbicide applications, species diversity was similar among the plots while relative species dominance differed strongly. Similarly, Biring *et al.* (2003) reported that 10 years after repeated manual cutting and a single application of glyphosate in a mixed-shrub community in British Columbia, total vegetation cover and species diversity remained similar, but community structure was altered with a reduction in the percentage cover of *Populus balsamifera*, an increase in the percentage cover of *Picea engelmannii* and differences in the percentage cover of other conifers, shrubs and herbs. It has been reported that multiple herbicide applications for woody plant control over several years during establishment has the potential to decrease species richness of *Pinus* plantation communities for up to 15 years (Miller *et al.*, 2003a). Further, Schabengerger and Zedaker (1999) in Virginia (USA) found that canopy diversity was inversely related to pine yield 12–14 years after a range of competition control treatments was tested. Herbaceous control had less longer-term influence than woody plant control in both investigations, while woody control treatments often initially increase richness of herbaceous species but can permanently decrease long-term woody plant diversity (Miller *et al.*, 2003a). It is also noteworthy that low rates of herbicide can suppress certain species, hence changing dominance, even if species are not actually killed (Boyd *et al.*, 1995; Miller *et al.*, 1999).

Mechanical treatment

Mechanical treatments can be effective in controlling woody competitors and particularly tall shrubs and understorey trees (Gjerstad and Barber, 1987; Walstad *et al.*, 1987; Bovey, 2001). When the goal is only to reduce the competitive pressure of hardwoods, mechanical treatments can completely suppress hardwood stems. When the goal is to reduce the competitive pressure of hardwoods while maintaining their beneficial effects on seedling morphological quality, the treatment will release only the top of the crop trees from light competition (Collet *et al.*, 1998). In most cases, the treatment only temporarily (Fiddler and McDonald, 1991; McDonald and Fiddler, 1993) removes the hardwood and shrub above-ground parts unless root dislodging implements are used. Moderate mechanical methods (e.g. cutting) yield moderate increases in growth of crop trees but less drastic changes to richness and structure than more intensive methods such as burning or herbicides (Locasio *et al.*, 1991; Lautenschlager *et al.*, 1998; Haeussler *et al.*, 1999). McDonald and Fiddler (1993) have stated, 'In most instances, forests cannot be managed economically without herbicides if the goal is to grow seedlings at the potential of the site and the plant community includes sprouting hardwoods and shrubs or rhizomatous forbs and ferns'.

Other mechanical treatments such as mowing may induce significant changes in species composition. Some herbaceous species, being capable of vegetative spread, are tolerant of mowing and will be favoured by mowing in comparison with other species. These species (often grasses) are very competitive for below-ground resources and have a very harmful effect on trees (Davies, 1987). Willoughby and McDonald (1999) reported such an effect in a 5-year experiment of afforestation of previous agricultural land in England, with the increasing development of *Trifolium repens* and *Lolium perenne* in the mown treatment in comparison with the unmanaged control treatment dominated by tall perennial species such as *Senecio jacobea*.

Soil cultivation has various effects on vegetation depending on the site characteristics and the tool used. For example, in young stands characterized by a high light availability at the ground level, destroying the vegetation by a disc plough is often reported to have no effect (on *Populus* sp. stands; Berthelot *et al.*, 2002) or to increase species richness (on *Populus* sp. stands; Laquerbe, 1999). Plant communities are generally different from the untreated control with a higher proportion of annual and biennials species (Berthelot *et al.*, 2002). After annual cultivation treatments end, species richness generally decreases and perennial species progressively establish.

Finally many different types of organic or inorganic mulches can be used to prevent vegetation development around the crop tree, the main aim often being to improve soil water or nutrient availability (Davies, 1987; McDonald and Helgerson, 1990; Fiddler and McDonald, 1991; McDonald and Fiddler, 1993; McDonald *et al.*, 1994; Van Lerberghes, 2004). The quickness of vegetation come back and its specific composition depends on the duration of the material used as mulch, the soil seed bank and the shade resistance of the plant species covered by the mulch.

Alternative silvicultural systems, thinning intensity and understorey vegetation composition

Partial cutting systems (e.g. shelterwoods, group selection and strip cutting) are practices increasingly used to regenerate forest stands in some forest regions, in association with planting or natural regeneration (Martin and Hornbeck, 1990; Ruark, 1990; Hannah, 1991; Tubbs and Lamson, 1991; McDonald and Fiddler, 1993; Lieffers and Stadt, 1994; Riegel *et al.*, 1995; McDonald and Reynolds, 1999; Holgen and Hanell, 2000; Wetzel and Burgess, 2001). Clearcutting has a greater potential for soil disturbance than other uneven-aged silvicultural systems, inclusive of shelterwood or group selection cutting (Turcotte *et al.*, 1991; Reynolds, 1992). Disturbance exposes bare mineral soil, producing a fertile seedbed for potential competitors (Roberts and Dong, 1991, 1993). Coupled with maximal light availability following clearcutting, optimal conditions prevail for regeneration of potential plant competitors. Regeneration systems other than even-aged clearcutting offer less reliance on herbicides for controlling these competitors, since they create less favourable light and soil disturbance conditions that enable the early establishment of severe plant competitors. In many cases after a clearcut, vegetation is composed of very competitive species (e.g. *Populus tremuloides*, *Calamagrostis canadensis*, *Epilobium angustifolium*, etc. in Alberta (Lieffers and Stadt, 1994); *Carex geyeri* and *Calamagrostis rubescens* in the Pacific Northwest (Riegel *et al.*, 1995)), making seedling establishment difficult or even impossible without vegetation control. The general idea supporting the practice of shelterwood, group selection, and strip cutting is that it is possible to avoid very competitive light-demanding species such as grasses, brambles, ferns and other invaders by limiting light availability to a threshold that still allows tree regeneration, even if seedling growth is not at its maximum (Martin and Hornbeck, 1990; Hannah, 1991; Reynolds, 1992; McDonald and Fiddler, 1993; McDonald and Reynolds, 1999; Schütz, 2004).

An example of this is the study conducted in *Larix* sp. stands in France and Belgium (Balandier and Pauwels, 2002; Figure 4). Two or three years after different thinning intensities, species diversity changed with relative light intensity (RLI) following a bell-shape curve from bare soil at very low RLI (<2 per cent) to a maximum for higher light availability (10–20 per cent) and to lower values for highest RLI (>20 per cent). The RLI value allowing maximum species diversity differs with stand type, site conditions and initial vegetation composition. The decrease in species diversity above the optimal RLI value can be explained by the rapid colonization of the total

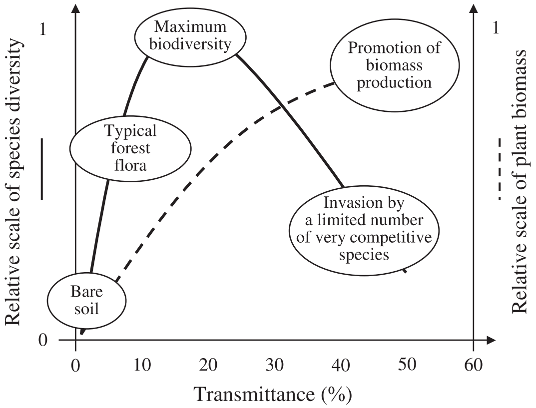

Figure 4. Evolution of the understorey plant species diversity and total biomass according to the light transmitted by the overstorey in larch (*Larix* sp.) stands in France and Belgium. Light availability at the ground level is given in relative value (transmittance), i.e. the value measured under the overstorey divided by the value measured above the overstorey; the relative scale of species diversity corresponds to the number of species found at a given transmittance value divided by the total number of species found on a site whatever the transmittance value is; and the relative scale of plant biomass corresponds to the biomass recorded for a given transmittance value divided by the maximum biomass recorded whatever the transmittance value is (adapted from Balandier and Pauwels, 2002). Plant species diversity peaks at about 10–20 per cent transmittance; light limits species number under this value and promotes the plot invasion by a small number of light-demanding species above it. Plant biomass is at maximum with the occurrence of the small number of light-demanding species and does not coincide with the maximum of biodiversity. Of course, transmittance values above 20–30 per cent are not favourable to tree regeneration because they promote the occurrence of a high density of very competitive species.

stand by a limited number of opportunistic and monopolistic species such as *Pteridium aquilinum*, *Rubus fruticosus*, *Calluna vulgaris*, and several graminoids. Many studies have reported such a colonization of forest stand by competitive species with high light availability (Alaback and Herman, 1988; McDonald and Reynolds, 1999) and often this fact is explained by the competition intensification among species with the increase in resources (e.g. Grime, 1994; Thomas *et al*., 1999). Of course the vegetation found in the highest light percentages (close to clearcut conditions) can lead to a complete standstill or at least to a severe slowdown of the succession (Frochot *et al*., 2002). It is noteworthy that in addition to the appearance of these competing species, their biomass and cover are promoted by the high light availability (Balandier and Pauwels, 2002; Figure 4). It is clear from this study that RLI values greater than 10–20 per cent should be avoided in order to promote seedling establishment and growth.

Another example of such a bell-shaped curve of species diversity is given by Jobidon *et al.* (2004). Stands of *Picea mariana* were established in the Québec region with different intensities of mechanical vegetation control and pre-commercial thinning. As the proportion of *Picea mariana* increased in the stand to the detriment of non-crop trees, total species richness and plant diversity first increased to a maximum and then decreased. By contrast to the previously cited study on larch, these variations of species richness and diversity are more due to the composition of the upper stratum and particularly non-crop tree diversity rather than to the composition of the intermediate and lower strata.

In another study, Klinka *et al.* (1996) in West Vancouver Island forests (Canada) observed an increase in the shrub layer (mainly *Gaultheria shallon* and *Rubus spectabilis*) with increasing light in the 6 years following canopy opening, while the herb and moss layers were not affected, probably because of the shade created by the shrub layer. Similar results were found in eastern Canada by Wetzel and Burgess (2001) with an increase in shrub diversity 2 years after a thinning but no change in the herb layer.

Light is not the single resource that affects understorey vegetation composition and cover and drives competition between vegetation and crop tree. Below-ground resource availability may lead to different responses of the understorey vegetation to light availability and to contrasted effects on crop trees (Lindh *et al*., 2003). This was clearly demonstrated by Riegel *et al.* (1995) in north-eastern Oregon where a reduction in tree canopy cover (*Pinus ponderosa*) was conducted in a split-plot study with or without root trenching to remove below-ground competition. Some species responded positively to light, others positively to an increase in soil resources, and some to both factors. In a literature review, Ricard *et al.* (2003) observed that contradictory results were reported on the subject. They noticed that, since the relative importance of competition for below- or above-ground resources depends on resource availability, the competitive effects of understorey vegetation against the seedlings and its changes with RLI vary with the site water and nutrient availability. Therefore optimal shelterwood density to control the vegetation and improve crop trees is site dependent.

Consequences regarding FVM

General considerations

As shown in the previous sections, the size, habit, density and growth rate of competing plants influence crop trees in different ways. Crop trees rarely compete with a single plant species, and the combined effects of competitors are difficult to analyse. Furthermore, the possible competitors for the crop trees on a given site are numerous, and the effective species composition of the competing vegetation is very difficult to predict because of the intrinsically stochastic nature of species establishment. As stated in the previous sections, there are, however, general patterns in the competitive effects of the various species summarized in Table 1 (Frochot *et al.*, 2002) by growth forms into five groups. Generally, graminoids, and to a lesser extent forbs with a dense cover, are more detrimental in the first years after stand establishment and mainly compete for below-ground resources, while shrubs and trees compete for light later in the rotation. A conceptual model, resulting from and summarizing, to a certain extent, the knowledge gathered in the previous sections, is proposed in Figure 5a and b.

At later stages in the rotation, a considerable number, cover, or density of herbaceous plants can exist in forest stands without appreciable (detectable) declines in crop tree yield. This is especially true if a weed-free zone, immediately adjacent to crop trees, is established early in the rotation (Carter *et al.*, 1984; Dougherty and Lowery, 1991; Richardson *et al.*, 1996). In many stands, herbaceous plants exist in the understorey throughout the rotation and their control leads to

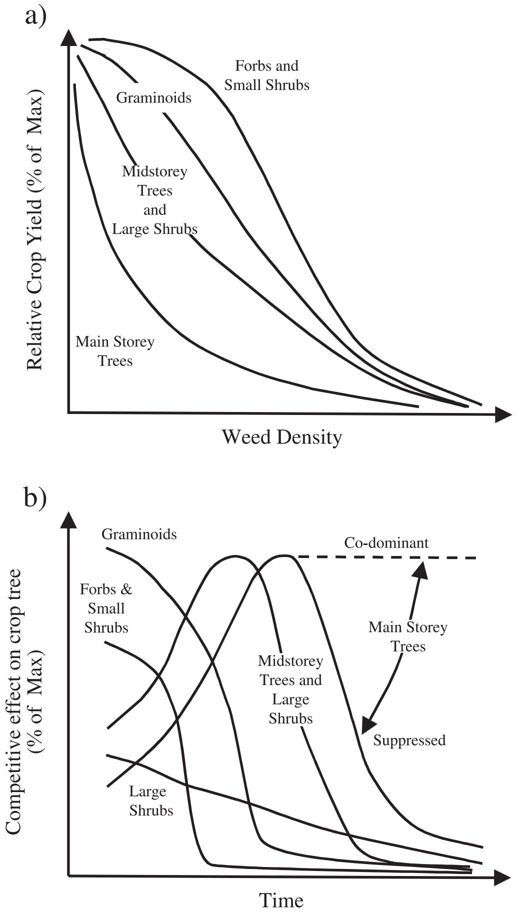

Figure 5. Proposition of conceptual models of (a) the influence of weed density independently of time and (b) the influence of time after stand establishment independently of weed density, on crop yield for different groups of competing vegetation. Crop yield is expressed as a percentage of maximum growth (supposed to be in the absence of competitive vegetation). (a) Small densities of forbs and graminoids do not affect yield of crop trees but depreciate it strongly at high density while a few individuals of mid-storey trees, large shrubs and main-storey trees lead to a significant loss of crop tree yield. (b) Graminoids and forbs compete early in the stand rotation but the depressive effect stops as soon as they are overtopped by crop trees, while the depressive effect of main-storey non-crop trees can last until the end of the rotation if they stay co-dominant with crop trees.

little or no yield gains. However, beyond a certain point of weed density, crop tree growth decreases rapidly and dramatically (Figure 5a). Conversely, even one weed tree in a forest canopy decreases the yield of crop species and an increasing number of weed trees in the canopy causes an exponential decline in crop yield (Figure 5a). Understorey shrubs and sub-canopy trees have intermediate effects. The reduction of seedling growth, even with the low densities of woody competitors, has been widely reported (e.g. Shainsky and Radosevich, 1991; Mitchell *et al.*, 1993; Perry *et al.*, 1993; Zutter *et al.*, 1998; Glover and Quicke, 1999; Bell *et al.*, 2000; Reynolds *et al.*, 2002a, b).

In many plantation settings, crop tree growth and yield are modelled as a function of stand age, the number of crop trees per unit area, and a site index curve. Differences in competition by different growth forms lead managers to use different models to assess the effects of weed control (Richardson *et al.*, 2005). As herbaceous weeds often delay crop tree establishment and growth in the first years after plantation establishment, but do not affect subsequent growth (i.e. treated and untreated stands take parallel paths with no further increase in time gain after the initial period), crop trees are often modelled as if they were older than their actual age (South *et al.*, 2005). Functionally, the herbaceous weeds retard growth until overtopped, but once that is achieved, the stand will grow at a rate determined largely by the number of trees and the site quality (site index). However, there are some cases where colonizing species such as perennial grasses can totally prevent crop tree establishment and growth (inhibition model of Connell and Slatyer, 1977; Kozlowski, 2002). Conversely, tree competition is modelled as a change in site quality; as if each weed tree present was reducing light or water and nutrient availability to the crop trees to a level that would be characteristic of poorer sites. The implication for shrub and sub-canopy tree impacts is that they could have an intermediate effect of retarding both stand development and also reducing ultimate long-term yield. In fact, a considerable body of evidence from yield studies in US southern yellow pine plantations points to this very effect. D'Anieri *et al.* (1986), Oppenheimer *et al.* (1989), Shiver and Daniel (1994), Fortson *et al.* (1996), Zedaker *et al.* (2002) and Albaugh *et al.* (2003) have demonstrated that the control of dense understorey shrubs and trees can lead to increased growth and yield in stands ranging from 15 to over 60 years old.

Principles of sustainable FVM

Competition control treatments can enhance crop trees while maintaining a diverse flora when the most severe competitors are specifically targeted and non-competitive components are permitted to remain as cohorts (Hartley, 2002).

Grasses and forbs are often early severe competitors of desired tree seedlings planted in open stands, due to their initial abundance. Grasses in general are more prevalent and can be competitive even on poorer sites with lower soil moisture and drier forest regions. Early control in the first and sometimes second years of both herbaceous components predictably yields greater crop seedling growth according to species, and sometimes improves survival on droughty sites (Wagner *et al.*, 1999). Suppression of grasses and forbs invariably will increase growth of cohort trees and increase their competitiveness along with crop trees but does not predictably enhance shrub growth (Miller *et al.*, 2003a). The initial presence of shrub and tree sprouts and crop tree seedlings suppresses grass and forb abundance and decreases competition for moisture. Therefore a planned balance of components (e.g. as sought by the shelterwood practice or spot control around seedling) can optimize crop tree growth, reduce suppression expenses, and provide habitat attributes.

Competition components of all types immediately surrounding the seedlings, have been found the most competitive for water, nutrients and light, especially for dense grasses in the first years. Control strategies that target competitors within 1–2 m of newly established seedlings are most efficient with minimizing herbicide use while conserving diverse plants outside these weed-free zones (Richardson *et al.*, 1996; Hartley, 2002). Graminoids and forbs contribute greatly to diversity in flora as well as providing habitat and food plants for vertebrates and invertebrates, and hence warrant conservation where possible. In a similar manner, small shrubs, while being less competitive than grasses and comparable to forbs with respect to density, often represent valuable food and habitat plants for forest fauna. McDonald

(1986) has reported that 'Grasses are not desirable in conifer plantations less than five years old, but after five years, they can aid conifer seedling growth by physically and chemically excluding more competitive vegetation. In plantations over 5 years old on good sites with deep soils, grasses can be beneficial by excluding deeper rooted shrubs.'

Abundant colony-forming shrub communities occur most commonly in boreal forests, montane forests, and in the sub-tropical coastal plain forests. These forest types require aggressive shrub control treatments to assure crop tree establishment and survival, either around seedlings or area-wide treatments. In both situations, shrub re-establishment from established rootstocks presents the most severe competition and can be the result of prior mechanical treatments. Other shrubs that become established from seed present less immediate competition but will influence seedling regeneration for a sustained period relative to tree and shrub growth rates. Those fruit- and heavy-seed-bearing shrubs are a principal wildlife food source and warrant consideration of partial control with moderate growth gains for habitat features.

Large shrubs and mid-storey trees have been less researched compared with the other growth-form components, while their values as fruit producers for fauna are widely recognized. Dense resprouting components exert competition immediately surrounding seedlings but their competitive influence decreases as plantations or stands develop with dominating crop canopies. Suppression treatments that facilitate later stand participation warrant consideration and further research and development.

Main-storey trees present the most formidable long-term component capable of completely superceding crop tree growth depending upon the relative dynamic canopy position. Low densities are capable of exacting significant growth losses to crop seedlings, depending upon the seedling's shade tolerance. Control treatments should be adjusted relative to anticipated or actual early competitor densities. Conversely, main-storey trees grown with hardwood crop seedlings have been shown to be valuable for improving form and knot reduction in the wood as well as having value for fruit and seed production. In shelterwood regeneration, main-storey trees must be managed to create conditions to favour regeneration over competitive understorey plants.

These principles are generalizations that will need modification relative to various forest regions, sub-regions, topography and site, while providing summaries of numerous research endeavours to guide management and future research.

Future research needs

It is noteworthy that now we have a large database showing that early control of the herbaceous or woody vegetation has long-term effects on crop trees, most noted are increases in wood yield (Wagner *et al.*, 2005). However, whilst there are instances where the necessity to control the vegetation is obvious, for instance in the situation of a dense layer of perennial grasses preventing any tree establishment, this requirement is not universal. Moreover Haeussler and Bergeron (2004) emphasized that small changes in the variability of plant communities today may have dramatic implications for forest composition, biodiversity and ecosystem functioning later. Miller and Miller (2004) amplify these concerns for forest regions that see intensification of FVM during this period of increasing forest fragmentation. As a consequence, designing vegetation management treatments or silvicultural operations for seedling establishment or crop tree growth requires the consideration of the evolution of the vegetation over several years, and across landscapes and regions, before it is possible to conclude on its potential interest or adverse effect. In addition, with the observation of early growth responses of planted trees to vegetation control, patterns and processes of plant succession on a long-term basis should be taken into consideration as this can have late repercussions such as a delay in canopy closure (Groninger *et al.*, 2004). Multiple-scale investigations are needed to examine the repercussions to ecological services and biodiversity exacted by various FVM strategies and especially comparing those anticipated by economic and policy developments.

It is also clear that we need an international common framework and requirements in studies aimed at characterizing the traits that confer competitive ability to a plant in the forest environment. Research using common protocols is more apt for providing the insights required to adjust our groups of competitive plants in different environments in order to adjust treatments and determine when treatments are justified. However, we also emphasized the necessity to include longer-term vegetation dynamics in studies dealing with influences of forest vegetation on crop trees because the intensity and orientation of competition change with floral composition in time and in space. The complexity of the flora in any region warrants more detailed taxonomic guides and keys such that current and future researchers are capable of accurately documenting the diversity.

Finally the role of biotic agents such as animals (and especially grazing animals, see Fiddler and McDonald, 1991; McDonald and Fiddler, 1993), insects, microorganisms and other forest inhabitants have not been examined in any detail in this paper. Following Connell and Slatyer (1977), we recognize that they play a fundamental role in interactions between plants and trees. It is a challenge to include them in future studies. It challenges us to understand the full array of interactions and life webs that connect all components within forest stands in order to develop realistic, efficient and sustainable forest practices crucially needed to supply goods, services and habitat for the swelling world population.

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