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ASPEN DYNAMICS AFTER HARVESTING IN BOREAL CONIFEROUS FOREST OF NORTHWESTERN QUEBEC

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RÉSUMÉ

Des études antérieures ont montré que les trembles (*Populus tremuloides* Michx) envahissaient progressivement les peuplements auparavant dominés par les conifères après la récolte. Les pratiques de récolte créent des perturbations sur une large gamme d'échelles spatiales et d'intensités, et on ne sait pas comment les différentes pratiques favorisent l'invasion des trembles dans les forêts des épinettes noires (*Picea mariana*). Une meilleure compréhension de la façon dont les traitements sylvicoles affectent le recrutement des trembles dans les peuplements de conifères est nécessaire pour pouvoir modifier nos pratiques d'aménagement forestier afin d'éviter ce problème. Le tremble étant une espèce clonale qui a la capacité de se régénérer de façon végétative ou sexuée, il est également important de connaitre l'impact des pratiques forestières sur la diversité génétique et génotypique de l'espèce. L'objectif principal de ce travail était d'étudier la relation entre les différents niveaux d'intensité de récolte (CPRS avec scarification du sol [CPRS-S], coupe avec protection de la régénération et des sols [CPRS] et coupe partielle [CP]), sur le mode de recrutement (végétatif ou sexué) et la densité post-récolte des trembles, et enfin sur les diversités génétiques et génotypiques des trembles envahissant les peuplements de conifères récoltés. Il a également été testé comment l'épaisseur de la matière organique (LFH), la classe de drainage, le pourcentage de couverture de débris ligneux et d'arbustes affectaient la densité et le mode de régénération des trembles dans les forêts de conifères. Le mode de recrutement des trembles a été déterminé par l'analyse dendrochronologie et cinq loci microsatellites ont été utilisés pour identifier et caractériser la diversité génétique et clonale post-récolte. La densité de la régénération des trembles a varié significativement entre les trois traitements de récolte, mais elle était sans rapport avec le gradient d'intensité de la perturbation. La grande majorité de la régénération était issue de semis dans deux méthodes de récolte (CPRS-S et CPRS), alors qu'elle était issue du drageonnement dans le traitement CP. Même si les variables environnementales (épaisseur LFH, la classe de drainage et le pourcentage de couverture des arbustes) ont influencé significativement la densité et le mode de régénération des trembles, elles n'expliquaient que très peu de la variation et étaient donc inefficaces pour prédire la densité des trembles et leur mode de régénération. Des niveaux élevés de variabilité génétique et génotypique ont été observées dans tous les traitements de récolte, et cette variabilité était équivalente entre les traitements de récolte ainsi qu'entre les modes de recrutement des trembles, sexué ou végétatif. Nous concluons que les différences dans les modes de recrutement des trembles et la densité post-récolte étaient davantage liés aux conditions de pré-récolte plutôt qu'à l'intensité de la récolte.

Mots clés : *dynamique peuplier faux-tremble, invasion tremble, structure génétique, diversité génotypique, peuplier faux-tremble*

ABSTRACT

Previous studies have shown that aspen (*Populus tremuloides* Michx) trees were gradually expanding into previously conifer-dominated stands after harvesting. Harvesting practices create disturbances on a wide range of spatial scales and intensities, and it is not known how different practices favour aspen invasion into black spruce (*Picea mariana*) forests. A clear understanding of how silvicultural treatments affect recruitment of aspen into coniferous stands is required to be able to modify forest practices in order to avoid conversion of previously coniferous stands into mixed or deciduous stands. The main objective of this work was to study the relationship between different levels of harvesting intensity (clear cutting with scarification [CPRS-S], clear cutting [CPRS], and partial cutting [PC]), the mode of aspen recruitment, post-harvest aspen density, and aspen genetic diversity. A field study was established to test whether aspen regeneration density and its mode of regeneration (sexual or vegetative) could be affected by different levels of harvesting disturbance. It was further tested how organic matter (LFH) thickness, drainage class, percentage cover of woody debris, and shrubs affected aspen density and its mode of regeneration into previously coniferous forests. The mode of aspen recruitment was determined through dendrochronological analysis and five microsatellite DNA loci analyses were used for clone and genetic structure identification. Aspen regeneration density significantly varied between the three harvesting treatments, but it was however unrelated to the gradient of disturbance intensity. The vast majority of regeneration was of seedling origin in two harvesting methods (CPRS-S and CPRS), while it originated from root suckering in the PC treatment. Even though, the environmental variables (LFH thickness, drainage class and percentage cover of shrubs) significantly affected the density and mode of regeneration of aspen, they were inefficient in predicting aspen density and of recruitment mode. High levels of genetic and genotypic variability were observed that did not differ between the harvesting treatments and between the modes of aspen recruitment, sexual or vegetative. We concluded that differences in aspen modes of recruitment and density were more related to pre-harvest conditions rather than to the harvesting intensity.

Keywords: *aspen dynamics, aspen invasion, genetic structure, genotypic diversity, Populus tremuloides*

CHAPTER I

GENERAL INTRODUCTION

The North American boreal forest extends from the Pacific to the Atlantic coast, which represents one of the largest ecosystems on the planet. In Quebec, the boreal zone is easily the largest of all vegetation zones (Pothier, 2001), covering an area of around 1 million km^2, or 70% of Quebec's territory. The evergreen conifer black spruce (*Picea mariana* (Mill.) and the broad-leaved deciduous aspen (*Populus tremuloides* Michx.) are among the few dominant, commercially important tree species with a North American trans-continental distribution that grow in a wide range of sites. The two species have contrasting autecological and forest characteristics (Viereck & Johnston, 1990) and are typically part of characteristic ecosystems that differ in biotic community, abiotic environment, structure, function, complexity, interactions (Ewald, 2000) and usually occupy different successional positions during the stand initiation stage of stand development (Larsen, 1980; Burns & Honkala, 1990). The boreal forest of eastern Canada is an ecosystem in which ecological processes are controlled by disturbances such as fire that influence the vegetation composition and dynamics (Heinselman, 1981; Bergeron, 1991). However, in the last decades, harvesting disturbed as much forested stands within the boreal forest as fire (Chen & Popadiok, 2002). These disturbances create a mosaic pattern in the forest, characterized by a large variability in species composition (Roberts & Gilliam, 1995).

Aspen is a good example of early successional pioneer species (Perala, 1990). It is disturbance-dependent, fast growing, short lived, and requires high light environments for establishment and rapid growth (Perala, 1990; Shepperd, 2001). Aspen's high plasticity to different environmental conditions is evident from its wide geographic distribution, range of climates and sites, and association with many different species. Aspen is capable of reproducing from stump sprouts (Schier *et al.*, 1985) and seeds (Perala, 1990), but root suckering from the parent root system is the primary means of natural regeneration (Zasada *et al.*, 1992; Lieffers *et al.*, 2002; Frey *et al.*, 2003). Although, the capacity of aspen for producing seed is high, the seeds are short-lived, generally lasting for two or three weeks (Maini, 1968). The seedlings' establishment success has been thought to be influenced by the combination of wide expanses of gap opening, exposed mineral soil and an abundant source of water during seed germination and establishment (McDonough, 1979; Mitton & Grant, 1996). Despite abundant seed crops (Bell, 1991), most authors report that seedlings establishment is relatively rare, although it has often occurred in post-fire stands (Kay, 1993; Romme *et al.*, 1997, 2005; Turner *et al.*, 2003). Reproduction is thus assumed to occur mainly asexually through root suckers following major disturbances. Asexual reproduction leads to clonal stand structure, in which one clone (genet) may consist of several trees (ramets). Disturbances that damage, cut or kill stems trigger root suckering, allowing for rapid stand regeneration (Jones & DeByle, 1985; Shepperd, 1990).

1.1 Stand dynamics and structure after harvest

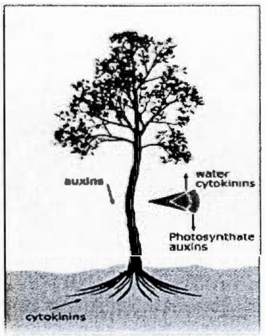
Forest harvesting produces different environmental conditions that can create different patterns of stand regeneration. Since 1995, silvicultural practices have been clearly directed toward harvesting with protection of pre-established regeneration and soils (CPRS), an approach intended to preserve some features of pre-harvest stand composition and structure (Government du Québec, 1996). It has replaced conventional clear-cutting in the boreal forest. When regeneration is insufficient to ensure forest renewal, the harvested blocks are scarified and then planted (CPRS with scarification). However, in the last two decades, there is more concern about the increase of hardwood presence in post- compared to pre-harvest stands (Jeglum, 1983; Reich *et al.*, 2001; Greene *et al.*, 2002; Laquerre *et al.*, 2011). These concerns have led to experiment other harvesting practices such as partial-cutting (PC), which may be better to control competitor vegetation (aspen) and improve seedling establishment (conifers). Partial cutting treatments maintain a continuous uneven-aged forest stand cover by harvesting a limited number of trees of various sizes and ages over time. The influence of the harvesting on patterns of tree species depends not only upon the level of environmental variability, but also on the change in eco-physiological responses through time. Thus, tree species of varying successional status exhibit differences in eco-physiological responses.

Stand initiation following disturbances (clear-cutting with scarification, clear-cutting or partial logging) results from the important changes that these disturbances cause in the forest stand structure. Their occurrence often leads to the complete removal of the canopy, complete or partial removal of the under-story and ground vegetation, and elimination and (or) disturbance of forest floor, creating favorable environmental conditions for the establishment and growth of a new forest stand (Keenan & Kimmins, 1993). However, these compositional differences often result in the increased presence and (or) abundance of many pioneer species following harvesting activities (Carleton & MacLellan, 1994; Reich *et al.*, 2001). Aspen is a strict pioneer species that often have higher light-saturated gas exchange rates of photosynthesis compared to late successional species (Bazzaz & Carlson, 1982; Kubiske & Abrams, 1993, 1994). Black spruce, on the other hand, is considered a shade-intolerant species that grows best in full sunlight but is capable of surviving for long periods at low light intensities (Heinselman, 1957, 1981). In general, the species adapted to high resource environments have high potential rates of resource capture and growth relative to species characteristics of low resource environments. In this condition, aspen often colonizes high-light early-successional sites (Reich *et al.*, 1998). On the other hand, low potential growth rate is presumed to be an acclimation to habitats characterized by low resource availability (Chapin, 1980; Reich *et al.*, 1992), such as shaded and nutrient poor environments in which black spruce is a good example.

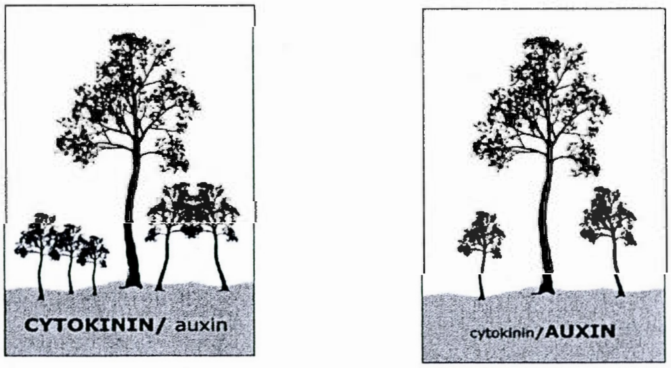
1.2 Dynamics of aspen regeneration after harvest

Dynamics of aspen regeneration varies based on stand structure before harvesting; if addressed jointly, the characteristics of stand pre-harvest and aspen's eco-physiological behavior influenced by environmental factors after harvesting, provide a perspective to understand aspen dynamics. As discussed earlier, aspen is disturbance-dependent and can regenerate at very high densities, sometimes exceeding 100,000 stems per hectare at age 2 (Steneker, 1976; Bella, 1986). Most suckers arise in the first year after a major disturbance, and a small proportion of suckers originate in the second and third growing seasons (Schier & Campbell, 1978). Most suckers originate from lateral roots that are closest to the surface of the soil (Peterson & Peterson, 1992). Root distribution is likely the primary reason for the high variability in sucker establishment by determining the environment for sucker initiation and the susceptibility of roots to disturbance (Shepperd. 1993). The processes controlling suckering are well known and documented (Frey *et al.*, 2003). These processes include the disruption of apical dominance (Horton & Maini, 1964; Steneker, 1976; Perala, 1977; Doucet, 1989; Navratil, 1991; Peterson & Peterson, 1992), increased soil temperature (Horton & Maini, 1964; Zasada & Schier, 1973; Doucet, 1989) and increased light availability (Doucet, 1989; Navratil, 1991). Apical dominance refers to the balance of auxins and cytokinins in the roots. Auxins, which suppress the production of suckers, are produced in the above-ground parts of the tree at the apical meristem (Farmer, 1962; Bancroft, 1989). Cytokinins, which are hormones produced in the root tips, promote suckering (Navratil, 1991). The interruption of the flow of auxins to the roots, caused by the tree harvesting or root injuries, causes a disruption of the ratio between these two hormones, thereby triggering sucker initiation (Navratil, 1991). High auxin to cytokinin ratios suppress suckering, while a low ratio promotes sucker initiation (Navratil & Bella, 1988; see Figure 1.1).

The presence of mature aspen trees after harvesting has been found to have a significant impact on sucker initiation (Schier & Smith, 1979; Schier *et al.*, 1985). Since most trees in a mature stands are physically interconnected through their root system in the boreal forest (DesRochers & Lieffers, 2001), hormones that inhibit sucker initiation may continue to be transported from residual aspen trees to most of the root system, limiting suckering. In this regard, partial cutting methods (PC) appear as good solutions to limit sucker initiation and growth of aspen suckers (Gifford, 1967; Schier & Smith, 1979; Ffolliott & Gottfried, 1991; Huffman *et al.*, 1999). PC also creates low light availability in post-harvest stands, limiting photosynthesis (Landhäusser & Lieffers, 2001) and shading out competitors sufficiently to allow establishment of coniferous seedlings (Lieffers *et al.*, 1993). On the other hand CPRS or CPRS-S will significantly increase light and soil temperatures, which might enhance sucker production and growth (Maini & Horton, 1966; Hungerford, 1988). Likewise, the scarification process removes litter protecting the root system that should also lead to enhanced sucker production (Kemperman, 1978).



Cytokinin/ Auxin movement in aspen



Cytokinin/ Auxin ratio and its effect on suckering

Figure 1.1 Cytokinin/ Auxin movement in aspen and its effect on suckering
(From: Navratil & Bella, 1988)

1.3 Aspen genetic structure

In general, population genetics theory suggests that variation in genetic structure increases with species environmental variation, population size, and range. It is thus not surprising that aspen is considered a genetically diverse tree species (David *et al.*, 2001; Madritch *et al.*, 2006). Aspen has separate male and female flowers (i.e. dioecious), and wind pollination ensures great levels of genetic diversity (Burns & Honkala, 1990; David *et al.*, 2001). The wide genotypic variability in aspen that results in equally wide phenotypic variability among clones is important to the ecology and management of this species. Aspen genetics studies may aid us in understanding explanatory mechanisms for the species' great adaptability to varying environments. This large clonal diversity is reflected in different patterns of carbohydrate reserves in roots (Schier & Johnston, 1971), suckering capacity (Schier & Campbell, 1980), and growth rates between clones (Barnes, 1969).

Genetic variation has two important consequences at the population level: heterozygosity tends to increase fitness of individuals, and genetic variation provides the evolutionary potential for populations to track environmental fluctuations and persist over time in stands (Lynch & Lande, 1993; Burger & Lynch, 1997). Therefore, if addressed jointly, genetics and ecology provide a powerful analytical approach to understanding and managing aspen. Aspen stands are often composed of clones of various sizes with numerous genetically identical stems (ramets). The size of aspen clones varies geographically, generally smaller in the east and larger in the arid intermountain west. Most clones in eastern North America are relatively small, usually less than 0.04 ha in size (Barnes, 1969; Wyman *et al*., 2003), while in the west the typical size have been reported to be up to 43 ha in size that contained 47 000 ramets (Kemperman & Barnes, 1976). If clones are large, some areas may have only a few individuals (clones) available for sexual reproduction (seedling establishment; Strain, 1964). In much of the West, even where there are many genotypes, the rarity of successful sexual reproduction results in restricted gene recombination, and therefore, very limited selection of new genotypes. In Quebec, Wyman *et al*., (2003) used a newer technique, microsatellite loci analysis, to examine clonal intermixing in stands. They discovered that suckers from different genotypes are likely to be highly intermixed after disturbance with ramets of different genotypes. This same high level of genetic variation has been confirmed in following researches (Namroud *et al*., 2005, 2006; Jelinkova *et al*., 2009), that have concluded that the gene pool established at the origin of the stands was considerably large.

The dynamics of aspen genetic structure may vary between different methods of harvesting, based on the mode of aspen recruitment (seedling or sucker). If populations of clonal species experience limited seedling recruitment, their genetic diversity is supposed to decline (Pornon *et al*., 2000; Moriguchi *et al*., 2001), whereas those with repeated seedling recruitment should maintain high genetic diversity (Chung *et al*., 2000; Stehlik &

Holderegger, 2000; Chung *et al.*, 2003; Ziegenhagen *et al.*, 2003). Recent work by Madritch and Hunter (2002), and Madritch *et al.*, (2006) suggests that loss of genetic variation within populations can influence the community and ecosystem level processes. Within seedling-established aspen populations, the greatest loss of genotypes and genetic variation occurs during the stand initiation phase when density-dependent mortality is at its high (David *et al.*, 2001). On the other hand in clonally derived sucker stands, aspen genotypes are typically conserved following disturbance so long as sucker production and growth are sustained from one generation to the next and the overall area of sucker production is maintained (David *et al.*, 2001). In this respect, aspen genetics has begun to question previous assumptions about aspen life history; (*i*) could rare seedling establishment events be related to high genetic diversity, and (*ii*) could vegetative reproduction only maintain high genetic diversity of aspen populations? However, the actual change in genotypes, if any, associated with harvesting events is unknown or very poorly understood (Knowles, 1985; Rajora, 1996, 1999; Rajora & Pluhar, 2003; David *et al.*, 2001).

1.4 Research objectives

Recent studies have shown that from the early 1950s, aspen has been expanding northward in black spruce forest domain of western Quebec (Grondin *et al.*, 2000). Even in stands that contain small proportions of aspen, management problems result from the ability of this species to reproduce from root suckers and to rapidly invade and dominate cutover sites (Perala, 1977; Huffman *et al.*, 1999). In this context, Reich *et al.*, (2001) found that there was evidence that logging had increased the proportion of landscape dominated by aspen in southern boreal forest stands in northern Minnesota, USA. However, some authors (Chen & Wang, 2006) found no increase in hardwood density following careful harvesting (CPRS) in lowland black spruce forests of the Ontario claybelt. Other case studies in northeastern Ontario (Brumelis & Carleton, 1988; Carleton & MacLellan, 1994; Carleton, 2000) and northwestern Quebec (Grondin *et al.*, 2000, Laquerre *et al.*, 2009) however confirm aspen's northerly expansion into the black spruce forest.

Competition by aspen early after disturbance can significantly reduce conifer recruitment and growth, an effect that may reinforce the long-term dominance of aspen in asexually regenerating stands (Johnstone, 2005). Following disturbances (e.g., clear-cutting) that return stands to early seral stages (Bergeron, 2000); competition exerted by aspen reduces spruce growth and survival for the first several decades of stand development (Filipescu & Comeau, 2007). An increasing abundance of deciduous trees in managed boreal black spruce stands is often seen as a threat to the forest industry because black spruce has higher economic values. This project attempts to provide an extensive study of dynamics of post-harvest sites by looking at how different harvesting methods can decrease (or increase) the proportion of aspen regenerating into black spruce forests. We anticipate that more intensive harvesting treatments will increase the expansion of aspen in post-harvest stands, by allowing aspen to invade both as suckers and seedlings. The different modes of recruitment should in turn affect genotypic diversity of post-harvest populations.

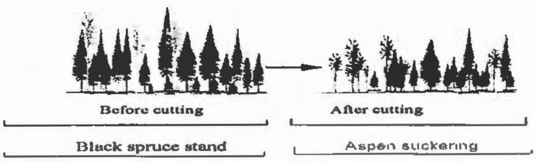
The second chapter of this thesis presents the results on regeneration of aspen into black spruce forests after three levels of harvesting (CPRS, CPRS-S and PC). The broad objective of this study was to examine the effects of different harvesting intensity (based on severity) on the dynamics of aspen invasion into coniferous stands. Comparisons were done between stands where different levels of disturbances were experimentally applied. The specific objectives were to (*i*) explain the occupation patterns of aspen after harvesting, (*ii*) identify the role of severity of harvesting on the mode of aspen recruitment, (*iii*) compare aspen genetic structure between the three levels of harvesting intensity, and (*iv*) examine the relationship between the modes of aspen recruitment with the genetic and genotypic structures. Our first hypothesis was that aspen would mainly regenerate through root suckering and that aspen density would increase with harvesting intensity. Three levels of disturbances represented by different harvesting treatments were tested:

a) *Light level of disturbance intensity - partial cutting* (PC): After partial cutting sucker recruitment would occur but less than in clear cutting with protection of regeneration and soils (CPRS) treatment and even less that in CPRS with scarification. In this method, it is possible to control aspen suckering by only partially opening the canopy (Jones, 1976; Hittenrauch, 1976; Schier & Smith, 1979; Ffolliott & Gottfried, 1991; Prévost & Pothier, 2003; see Figure 1.2a). On the other hand, there could be a reduction of the growth and survival of the suckers produced in partially-harvested stands because they receive limited light (Gifford, 1967; Huffman *et al.*, 1999; Prévost & Pothier, 2003).

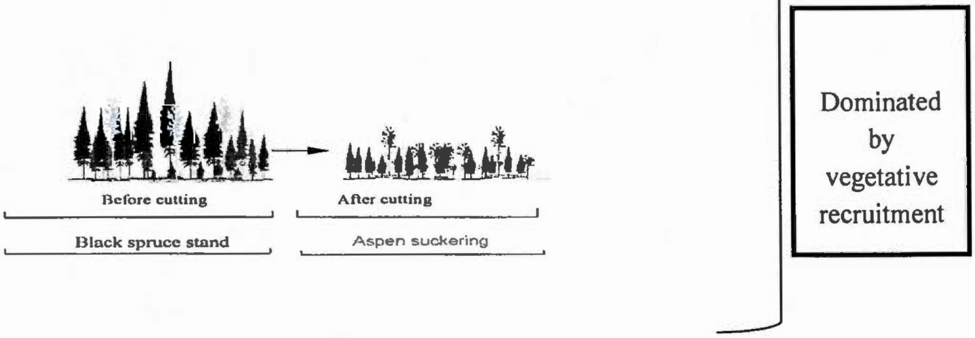
b) *Intermediate disturbance intensity - CPRS cutting*: this method removes all trees and also disturbs the soil surface or the roots themselves (Weingartner, 1980; Fraser *et al.*, 2003; Frey *et al.*, 2003), which should positively affect the initiation and early growth of suckers (Kemperman, 1978; Brown & DeByle, 1987; Denis *et al.*, 1994; Huffman *et al.*, 1999). This harvesting treatment should decrease the occurrence of seedlings; because it prohibits seed germination due to the thickness of organic matter that is left in undisturbed sites by the CPRS (see Figure 1.2b). It is well known that the worst seedbed for small-seeded species such as aspen is the presence of thick organic layers (Chrosciewicz, 1974; Johnson *et al.*, 1998).

c) *Severe level of disturbance intensity- CPRS with scarification*: This treatment should favor higher suckering because it removes the organic layer and represent a higher level of disturbance, which stimulates nutrient release and possibly enhances suckering and sucker growth (Frey *et al.*, 2003; see Figure 1.2c). In these conditions, regeneration by seed would occur because it creates exposed mineral soil, which is necessary for aspen seedling establishment (Zasada *et al.*, 1983; Prévost, 1996, 1997; Romme *et al.*, 2005).

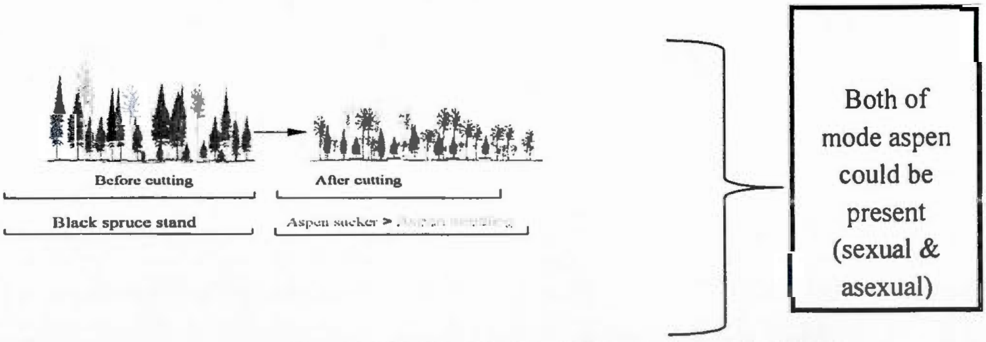
In relation to the genetic structure, the hypothesis was that there would be a relationship between the mode of aspen recruitment and aspen genetic structure, with an increase in genetic and genotypic diversity when both sexual and vegetative recruitment occur. Harvested black spruce forests that would favor vegetative propagation of aspen, should be occupied by a small number of aspen clones of larger size. If we assume that the regeneration was mostly by suckering after cutting, the genotypes should be maintained but increased in size with the recruitment of many suckers. However, in methods where aspen seedling recruitment also occurs, the presence of many aspen clones of smaller size should be observed. The mode of aspen recruitment was determined through dendrochronology, and microsatellite loci analysis was used to identify the genetic and genotypic structures of aspen in 2 post-harvest black spruce stands. We also measured the main environmental factors (drainage class, organic matter layer thickness, the percentage cover of woody debris, and shrubs) that could affect aspen regeneration.



a. Regeneration of aspen in coniferous stands (> 75%) after harvesting- PC



b. Regeneration of aspen in coniferous stands (> 75%) after harvesting- CPRS



c. Regeneration of aspen in coniferous stands (> 75%) after harvesting- CPRS with scarification.

Figure 1.2 Regeneration of aspen in a conifer dominated stand after disturbance.

(From: Bergeron *et al.*, 2002)

CHAPTER II

THE IMPACT OF HARVESTING INTENSITY ON ASPEN RECRUITMENT AND GENETIC STRUCTURE IN A CONIFEROUS STAND

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2.1 Abstract

Various harvesting techniques produce different levels of disturbance and may affect the composition of post-harvest stands. In particular, current practices appear to favour the expansion of early successional species such as aspen (*Populus tremuloides* Michx) in previously conifer-dominated stands. The aim of the present study was to determine and compare the density and mode of aspen recruitment, genetic and genotypic diversities following harvesting with increasing the levels of intensity, from light to severe: (*i*) partial cutting (PC), (*ii*) cutting with protection of regeneration and soils (or careful logging, CPRS), and (*iii*) CPRS with soil scarification (CPRS-S). The mode of aspen recruitment was determined through dendrochronological analysis and five microsatellite loci were used to identify and characterize aspen genetic and genotypic diversity. Aspen density and seedling presence were characterized as a function of disturbance intensity, organic matter (LFH) thickness, drainage class, percentage cover of woody debris and shrubs. Aspen regeneration density significantly varied in the three disturbance intensities ($P \leq 0.05$), ranging from 22,707 to 21,718 and 6, 309 stems ha^{-1} in CPRS-S, PC, and CPRS, respectively. The presence of aspen seedlings was best predicted by the disturbance intensity (harvesting treatment), with greater number of seedlings in CPRS-S, and CPRS, compared to PC, while the majority of aspen in PC was recruited through root suckering. In terms of genetic and genotypic variability, all stands maintained high levels of genetic diversity, which did not differ between harvesting treatments. Genotypic diversity was high in all treatments (G/N 0.87, 0.93, 0.89 in CPRS-S, CPRS and PC respectively), and most genets were unique. The small clone sizes suggested that aspen regeneration through seed is very common. High genotypic diversity found in PC can be explained by vegetative reproduction from different genotypes that existed in the pre-harvested stands. Consequently, the high genetic and genotypic diversities in aspen recruited after harvesting were unrelated to the mode of regeneration, through seed or root suckering.

Keywords: *root suckering, genetic diversity, genotypic diversity, Populus tremuloides, aspen expansion*

2.2 Résumé

Les traitements sylvicoles et notamment la coupe, produisent différents niveaux de perturbation et peuvent affecter la composition en espèces après la récolte des peuplements. En particulier, il semble que les pratiques actuelles favorisent l'expansion des espèces pionnières, comme le tremble (*Populus tremuloides* Michx) dans les peuplements auparavant dominés par les conifères. L'objectif de la présente étude était de déterminer et de comparer la densité, le mode de recrutement et la diversité génétique et génotypique du tremble, après la coupe à différentes intensités de perturbation, de légère a sévère : (*i*) coupe partielle (CP), (*ii*) coupe avec protection de la régénération et des sols (CPRS), et (*iii*) CPRS avec scarification du sol (CPRS-S). Le mode de recrutement du tremble a été déterminé par analyse dendrochronologique et cinq loci microsatellites ont été utilisés pour identifier et caractériser la diversité génétique et clonale. La densité et le mode de régénération du tremble (sexué ou végétatif) ont été caractérisés en fonction de l'intensité de la perturbation, de l'épaisseur de la matière organique, de la classe de drainage, et du pourcentage de recouvrement des débris ligneux et arbustes. La densité de la régénération a varié significativement selon les trois intensités de perturbation ($P \leq 0.05$), allant de 22,707 à 21,718 et 6,309 tiges par hectare dans la CPRS-S, CP, et la CPRS, respectivement. La présence de tremble a été le mieux prédite par l'intensité de la perturbation, avec un plus grand nombre de semis dans la CPRS-S, et la CPRS, par rapport à la CP, alors que la majorité des trembles dans la CP a été recrutée par drageonnement. En termes de variabilité génétique et génotypique, tous les traitements de coupe ont maintenu des niveaux élevés de diversité génétique, qui ne différait pas entre les traitements de récolte. La diversité génotypique était élevée dans tous les traitements (G/N 0,87, 0,93, 0,89 en CPRS-S, la CPRS, et CP, respectivement), et la plupart des genets étaient uniques. Les clones de petite taille suggèrent que la régénération du tremble par semis est commune. Une grande diversité génotypique dans la CP peut être expliquée par reproduction végétative de génotypes différents qui existaient dans les peuplements avant coupe. Par conséquent, la grande diversité génétique et génotypique de trembles recrutés après la récolte était sans rapport avec le mode de régénération par graine ou drageonnement.

Mots clés : *drageonnement, Diversité génétique, Diversité génotypique, Peuplier faux-tremble, Expansion peuplier faux-tremble*

2.3 Introduction

During the last few decades, forest harvesting has become increasingly important as a disturbance in the boreal forest of Canada. In Quebec's boreal regions, forests are mostly harvested by clear cutting with protection of regeneration and soils or careful logging (CPRS; Ruel *et al.*, 2000; Groot *et al.*, 2005); an approach intended to preserve pre-established regeneration and soil structure (Government du Québec, 1996). After harvesting where natural regeneration is lacking, soils are usually scarified (CPRS-S; CPRS followed by soil scarification) with forestry-disks before planting of conifer seedlings. These practices appear to favour the expansion of early successional species such as aspen (*Populus tremuloïdes* Michx) into previously conifer-dominated stands (MacIsaac *et al.*, 2006). The presence of aspen in conifer-dominated stands, even in small proportions is problematic for forest managers because this species quickly invades and dominates cutover sites (Perala, 1977; Doucet, 1979; Huffman *et al.*, 1999) and also reduces spruce growth and survival for several decades after harvesting (Filipescu & Comeau, 2007).

Following stand-replacing disturbances, aspen usually regenerates prolifically via root suckering (Bartos & Mueggler, 1981, 1982; Crouch, 1983; Brown & DeByle, 1987). Root suckering is triggered by a disturbance in apical dominance, when stem removal interrupts the flow of auxins from crowns to roots, thereby changing the hormonal balance in the roots (Schier *et al.*, 1985). Harvesting methods that kill or severe portion of lateral roots from parent trees can also cut off the auxin flow and initiate suckering (Shepperd, 1996, 2001, 2004). The quantity and distribution of aspen roots as well as pre-harvest stand conditions will have an impact on sucker density and viability after harvesting (Shepperd, 1993; Frey *et al.*, 2003). Sexual reproduction is thought to be rare in aspen due to low survival rate of seedlings (McDonough, 1979; Mitton & Grant, 1996; Latva-Karjanmaa *et al.*, 2003) and a narrow range of suitable seedbed conditions for germination (Barry & Sachs, 1968). However, some studies have shown that seedling recruitment could be more frequent than previously thought; this includes the presence of aspen seedlings in small gaps (Kuuluvainen & Juntunen, 1998; Jelinski & Cheliak, 1992) and regeneration from seed after severe fires (Romme *et al.* 1997; Stevens *et al.* 1999; Quinn & Wu, 2001). High genetic and genotypic variability in eastern North American forests also suggest a greater frequency of successful seed regeneration events (Jelinski & Cheliak, 1992; Mitton & Grant, 1996; Wyman *et al.*, 2003; Namroud *et al.*, 2005).

Different levels of canopy opening will modify external factors such as light, soil temperature and other environmental variables (Dalton & Messina, 1995; Lajzerowicz *et al.*, 2004) that may differently affect aspen regeneration density and mode of recruitment. The number of mature aspen trees retained after harvesting has been found to have a significant impact on the number of suckers formed (Schier *et al.*, 1985). Since aspen stems are typically interconnected by their parental root system (DesRochers & Lieffers, 2001), hormones that inhibit sucker initiation in intact forests may continue to be transported from residual trees to most of the root system in partially harvested stands (Schier *et al.*, 1985). However, as the number of residual parent trees decline, there is likely a decline in the maintenance of apical dominance in the root network. Previous studies have shown that it was possible to limit aspen suckering by only partially opening the canopy (Jones, 1976; Hittenrauch, 1976; Schier & Smith, 1979; Ffolliott & Gottfried, 1991; Prévost & Pothier, 2003). Moreover, the growth and survival of the suckers produced in partially-harvested stands are reduced because they receive limited light (Gifford, 1967; Huffman *et al.*, 1999; Prévost & Pothier, 2003). Disturbances that remove all trees (e.g., CPRS, and CPRS-S) also disturb the soil surface or the roots themselves (Weingartner, 1980; Fraser *et al.*, 2003; Frey *et al.*, 2003), and this may affect the initiation and early growth of suckers (Kemperman, 1978; Brown & DeByle, 1987; Denis *et al.*, 1994; Huffman *et al.*, 1999). Canopy opening permits more light to reach the soil surface thereby increases soil temperature which may facilitate auxin degradation (Schier *et al.*, 1985; Hungerford, 1988) and promote sucker initiation (Ahlgren & Ahlgren, 1961; Maini & Horton, 1966; Hungerford, 1988). Soil scarification by machine traffic can also result in soil mixing and increased soil temperatures, which could stimulate nutrient release and possibly enhance suckering and sucker growth (Frey *et al.*, 2003). Further, removal of litter protecting the root system during the scarification process will also lead to an enhance sucker production (Maini & Horton, 1966; Weingartner, 1980; Alban *et al.*, 1994; Lavertu *et al.*, 1994; Frey, 2001), and contribute to seedling germination and establishment by exposing bare mineral soil (Zasada *et al.*, 1983; Prévost, 1996, 1997; Romme *et al.*, 2005).

In the present study we examined aspen recruitment in conifer-dominated stands following harvesting giving increasing the level of intensity, from light to severe: (*i*) partial cutting (PC), (*ii)* cutting with protection of regeneration and soils (CPRS), and (*iii*) CPRS with soil scarification (CPRS-S). The main objective of this study was to better understand the mode of aspen expansion into conifer-dominated stands following harvesting. Dendrochronological examination of aspen regeneration was used to determine their origin (sexual or vegetative), while molecular analysis was used to identify and characterize aspen genetic structure. We hypothesized that, (*i*) aspen regeneration density (sexual and vegetative) would be greater at higher levels of disturbance (CPRS-S) because of mineral soil exposure allowing seedling recruitment in addition to root suckering, while the other harvesting methods (CPRS and PC) would mostly favour vegetative propagation; (*ii*) the mode of aspen recruitment would impact genetic and genotypic diversity of aspen, with an increase in diversity observed when both sexual and vegetative recruitment occur.

2.4 Materials and methods

2.4.1 Study sites

The study was carried out in two sites of north western Quebec (48° 46' N, and between 78° 07' W to 78° 52' W). This region is part of the balsam fir-white birch (*Abies balsamea* (L.) Mill.- *Betula papyrifera* Marsh.) bioclimatic domain forest of western Quebec (Grondin, 1996). Black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), balsam fir, and aspen are the dominant tree species. Stand composition characteristics of the studied sites are presented in Table 2.1. Both stands were dominated by coniferous species (> 75% stems). Mean basal area was between 27.8- 11.4 m^2 /ha for spruce and 9.9-19.7 m^2 /ha for jack pine, while aspen basal area was 2.6 and 2.0 m^2 /ha at St-Dominique and Authier Nord, respectively (Table 2.1). The topography is relatively flat, and elevation is ca. 300 m above sea level. According to nearby weather stations in Amos, and La Sarre, Quebec (Environment Canada, 2004), mean annual temperature was 1.1, and 0.8° C and annual precipitation was 920 and 856 mm, for Saint-Dominique, and Authier-Nord, respectively.

Table 2.1 Summary of pre-harvest stand characteristics at two sites.

Site	Black & White spruce			Jack pine			Balsam fir			Aspen		
	N	*A*	*DBH*[1]	*N*	*A*	*DBH*	*N*	*A*	*DBH*	*N*	*A*	*DBH*
Saint-Dominique	1940	27.8	16	370	9.9	21	128	0.2	8	64	2.6	32
Authier-Nord	978	11.4	13	850	19.7	16	3	0	10	32	2.0	30

Note: N= mean density (stem/ha); A= mean basal area (m^2/ha); DBH= mean diameter at breast height. (1)Tree species (*DBH* > 2cm)

2.4.2 Sampling design

The regions of Saint-Dominique and Authier-Nord were harvested in fall 2002 and winter 2003. Three harvesting methods were used to harvest the stands in both regions: (1) Partial cut (PC), a non-intensive practice in which single trees or small groups are periodically logged, ensuring the presence of a continuous canopy, and preserving an uneven-aged and multi-layered forest over time; (2) Careful logging (CPRS), where all trees with a diameter of ≥9 cm are harvested, while restricting machinery traffic to corridors in order to protect pre-established regeneration and soils; (3) Careful logging with soil scarification (CPRS-S) where trees are harvested as in (2) and soil is later scarified to prepare for planting (i.e. disked to removed/disturb the organic layer down to the mineral soil). We considered these treatments as three levels of disturbance; light (PC), moderate (CPRS), and severe (CPRS-S). In summer 2006, we sampled a block of each treatment at every site using circular plots of 2 m in diameter. These plots were distributed every 5 m along a 120 m-long and 25 m-wide transect from the external circumference of a previous study site. This was done for a total 110 plots/treatment, with exception of CPRS-S where only 106 plots were made due to the proximity of some forestry roads, where sampling was impossible. Depth of organic matter on the forest floor (LFH layer), drainage class, percent cover of woody debris and shrubs were measured in each plot. LFH consists of an L-layer with fresh, intact, identifiable litter, an F-layer with fermenting, fragmented litter, and an H-layer with humus, i.e. decomposed plant residues (Packham & Harding, 1982). All aspen regeneration was tallied in each 2 m circular plot, and one aspen (when present, closest to the middle) was sampled for dendrochronological and DNA analyses.

2.4.3 Laboratory analysis

2.4.3.1 Dendrochronology analysis

The mode of aspen recruitment was determined by performing a dendrochronological analysis on each sampled aspen stem and corresponding root system. Aspen saplings were removed from the ground by cutting each individual at the base, and collecting it along with its lateral and tap roots. In total, 176 individuals were collected and processed. Growth rings were revealed by sanding sequentially with coarse to fine sanding paper (up to 400 grit). Small diameter stems and roots were prepared by cutting the surface with a sharp razor blade and filling the wood cells with white chalk. The mode of aspen regeneration was determined by comparing the number of annual growth rings of stems and their corresponding roots using a 10-60X power dissecting microscope; aspen suckers have fewer rings than their parental roots, while seedlings have more or the same number of rings than their roots (DesRochers & Lieffers, 2001).

2.4.3.2 DNA extraction and amplification

Five microsatellite DNA loci (Table 2.2) were used for clone identification and aspen genotyping (Dayanandan *et al.*, 1998; Rahman *et al.*, 2000). DNA extraction from leaf tissue using the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich Canada, Oakville, Ontario, Canada) according to the manufacturer's protocol. Genotyping of individuals were performed by screening five microsatellite primer pairs originally developed for aspen, *PTR*1, *PTR* 2, *PTR* 3, *PTR* 4, and *PTR* 8 fluorescent labelling 6-FAM, HEX, TET, 6-FAM, and HEX respectively. The five microsatellite loci were amplified using dye-labeled oligonucleotide primers and *Taq* polymerase (Gibco, Invitrogen Life Technologies Burlington, Ontario, Canada). Polymerase chain reaction (PCR) was carried out in a 96-well GeneAmp PCR System 9700 (Applied Biosystems, Foster City, California, USA) in a total volume of 10 μL containing 4 μL DNA extract, 0.625 pmol/μL primers, 0.2 mM dNTP, 3.125 mM $MgCl_2$, 1.4 μL BSA, and 12.5 mM Tris-HCl (PH 8.0). Fragment amplification started with 10 min at 95° C for enzyme activation and DNA standard denaturation, continued with 33 cycles of 1 min denaturation at 95° C, 1 min annealing at touchdown temperatures decreasing by 1° C every cycle from 60° C to 54° C, and 1 min primer extension at 72° C, and terminated with 7 min final extension at 72° C. The PCR product (0.4 μL) was mixed with 0.25 μL internal size standard (TAMRA 500 Liz) and 12 μL deionized formamide, and the mixture was heat-denaturated for 5 min. Fragments were separated by capillary electrophoresis in 3130 Genetic Analyzer (Applied Biosystems). Allele calling was done in GeneMapper version 3.7 (Applied Biosystems).

Table 2.2 Repeat patterns, primer sequence (F, forward and R, reverse), number (A), size range of alleles, and observed heterozygosity (H_O) at five microsatellite DNA loci (PTR 1, PTR 2, PTR 3, PTR 4, and PTR 8) in *Populus tremuloides.*

Locus	Repeat	Primer sequence	A	Size (bp)	H_O
PTR 1	$(GGT)_5N_{45}(AGG)_9$	AGCGCGTGCGGATTGCCATT	8	238-268	0.46
		TTAGTTTCCCGTCACCTCCTGTTAT			
PTR 2	$(TGG)_8$	AAGAAGAACTCGAAGATGAAGAACT	12	195-228	0.74
		ACTGACAAAACCCCTAATCTAACAA			
PTR 3	$(TC)_{11}$	CACTCGTGTTGTCCTTTTCTTTTCT	21	184-242	0.69
		AGGATCCCTTCCCTTTAGTAT			
PTR 4	$(TC)_{17}$	AATGTCGAGGCCTTTCTAAATGTCT	11	194-226	0.57
		GCTTGAGCAACAAACACACCAGATG			
PTR 8	$(A)_{11}$ $(CT)_8$	TAGGCTAGCAGCTACTACAGTAACA	9	132-150	0.18
		TTAAGTGCGCGTATCCCAAAGA			

2.4.4 Statistical analysis

2.4.4.1 Mode of aspen recruitment

One-way analysis of variance (ANOVA) was used to test differences in aspen regeneration density between the three harvesting treatments. When the ANOVA showed differences between the harvesting treatments, Turkey's multiple comparison tests were used. Data on aspen density were log-transformed to meet assumptions of normality of residuals.

Relationships between aspen regeneration density and harvesting treatments, LFH thickness, drainage class, % cover of woody debris and shrubs were examined with simple linear regression models (univariate) in R (v. 2.10.1, R Development Core Team 2008) using the lm function. We examined the independence of drainage in the two regions with Pearson's Chi-square and Fisher's exact tests (Thompson, 2009). The other numerical variables such as LFH thickness, % cover of woody debris and shrubs were examined with non-parametric Mann-Whitney U tests (Mann & Whitney, 1947).

Pearson's Chi-Square tests (Thompson, 2009) were used to test the equality of proportions (probabilities of success) of seedlings *vs*. suckers in the three types of harvesting. A logistic regression model was fitted to predict the presence aspen seedlings (Agresti, 2002) with the dependent variable (*logit;* the natural log of the odds), in the following form:

$$log\ odds\ = logit\ P\ = In\ \frac{P}{1-P}\ = \alpha + \beta x$$

Where the probability of aspen seedling presence (*P*) was mathematically equivalent to the following expression (α the intercept parameter, β the slope parameter and x the explanatory variable);

$$P = \frac{exp^{\alpha+\beta x}}{1 + exp^{\alpha+\beta x}}$$

Due to the presence of correlations between abiotic (LFH thickness, and drainage class) and biotic variables (% cover of woody debris and shrubs) with the harvesting treatments, a simple logistic regressions was used to explain the presence of aspen seedlings as a function of disturbance intensity (DI: harvesting treatments), LFH thickness, drainage class (good, moderate, and poor), % cover of woody debris, and shrubs. The goodness-of-fit of the model was assessed using a Le Cessie and van Houwelngen test (1991), while omission of important or inclusion of extraneous variables was checked using Cook's distances and hat values (Everitt & Hothorn, 2006). Independence of variables and randomness of residuals were also verified (Everitt & Hothorn, 2006).

Akaike's information criterion (AIC) (Burnham & Anderson, 2004) was used to identify the most plausible models explaining the presence of aspen seedlings. Differences in AICc values were calculated for the respective models relative to the "best" model, (i.e., the model with the lowest AICc. Models with ΔAICc < 2 and high Akaike weights (ω_i, interpreted as probabilities) were deemed to have the greatest statistical support (Burnham & Anderson, 2004). Furthermore, we assessed the power of best model by the Nagelkerke R squared value, to describe the proportion of the model's variance explained by the independent variables. All statistical analyses were performed using R (R Development Core Team, 2008), and the significance threshold was fixed at 0.05.

2.4.4.2 Genetic analysis

Number of alleles, heterozygosity levels, proportion of polymorphic loci, Hardy-Weinberg Equilibrium and *F*-statistics were computed using the Genetic Analysis in Excel (GeneAlEx.6), (Peakall & Smouse, 2006). Furthermore, a goodness of fit test (*G*-test) was performed on allele frequencies to test whether homogenously distributed over five loci in post-harvest stands. The genetic structure of the complete set of samples (within post-harvest) were investigated by an analysis of molecular variance (AMOVA), using genetic distance: number of different alleles obtained by calculating the weighted average F_{ST} over all loci (Weir & Cockerham, 1984; Michalakis & Excoffier, 1996). Basically, AMOVA allowed us to calculate the covariance components within and between samples.

We calculated the percentage of single ramet genets (a genet composed of only one ramet) and the number of multiramet genets (a genet composed of more than one ramet, called clones). Genotypic diversity was determined for each population as the *G*/*N* ratio, which is the proportion of different genotypes in a population, where *G* is the number of distinct clones and *N* is the total number of individual analysed (Pleasants & Wendel, 1989). The *G*/*N* value ranges from 0 to 1, where 0 reflects all individuals containing the same multilocus genotypes, and 1 is where each individual has unique multilocus genotypes.

2.5 Results

2.5.1 Aspen recruitment

Average aspen regeneration densities for two sites corresponded to 22,707, 6,309 and 21,718 (trees ha^{-1}) in CPRS-S, CPRS, and PC, respectively ($P \leq 0.05$). The regeneration density differed significantly between CPRS-S and CPRS, PC and CPRS-S, and PC and CPRS ($P \leq 0.05$; Table 2.3). Across all harvesting treatments, 62 % of the aspen regeneration was originating from seedlings. The proportion of seedlings was significantly different between the three harvesting treatments ($P < 0.001$); there was a higher percentage of aspen seedlings in CPRS-S and CPRS treatments (90% and 80%, respectively), while it was only 7% in PC (Figure 2.1).

Table 2.3 Mean aspen density (log-transformed) and confidence intervals in three harvesting treatments for two sites.

(I) Aspen density	(J) Aspen density	Mean difference (I-J)	P value	95% confidence interval Lower Bound	Upper Bound
CPRS-S	CPRS	0.65	<0.001	0.42	0.88
	PC	0.22	0.05	-0.01	0.44
CPRS	CPRS-S	-0.65	<0.001	-0.88	-0.42
	PC	-0.43	<0.001	-0.65	-0.21
PC	CPRS-S	-0.22	0.05	-0.44	0.005
	CPRS	0.43	<0.001	0.21	0.65

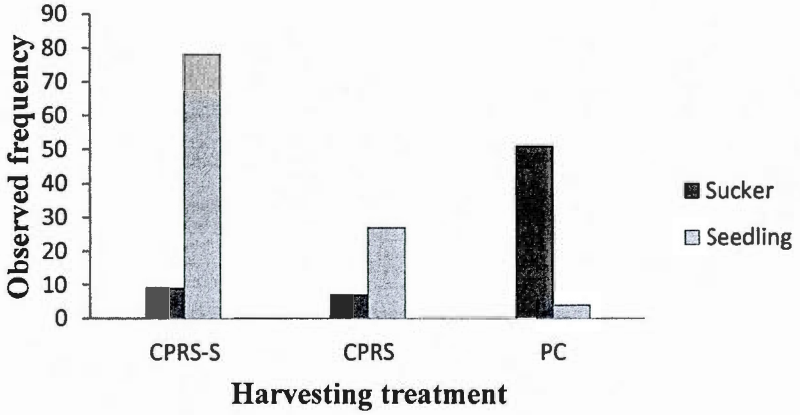

Figure 2.1 Frequency histogram showing distribution of seedlings and suckers in the three harvesting treatments at two sites.

The age of aspen seedlings ranged from 1 to 4 years old, while the majority of suckers established rapidly after harvesting (they were 3 or 4 years old) and had established from 12-18 years old parental roots (Table 2.4, Figures. 2.2 and 2.3).

Table 2.4 Minimum and maximum number of aspen in each 2 m circular plot, number of aspen sampled to identify mode of aspen recruitment, number of seedlings and suckers, and number of aspen sampled for genetic structure identification. (*Values are means with SDs given in parentheses)

Site	Harvesting treatment	Nb. Aspen (Min-Max)	Nb. Aspen sampled	Seedling			Sucker		
				Nb.	Mean age		Nb.	Mean age	
					Root	Stem		Root	Stem
Saint-Dominique	CPRS-S	0-40	49	40	1.9(0.5)*	2.2(0.5)	9	12.1(3.4)	3.1(0.7)
	CPRS	0-18	27	25	1.5(0.5)	1.8(0.5)	2	12(1.4)	3.5(0.7)
	PC	0-67	41	2	2.5(0.7)	3.5(0.7)	39	15(9.2)	2.9(0.9)
Authier-Nord	CPRS-S	0-15	38	38	1.5(0.5)	1.8(0.4)	-	-	-
	CPRS	0-36	7	2	1.5(0.7)	1.5(0.7)	5	15.8(8)	3.2(0.4)
	PC	0-55	14	2	2(1.4)	2.5(0.7)	12	18.5(10)	3.2(0.6)

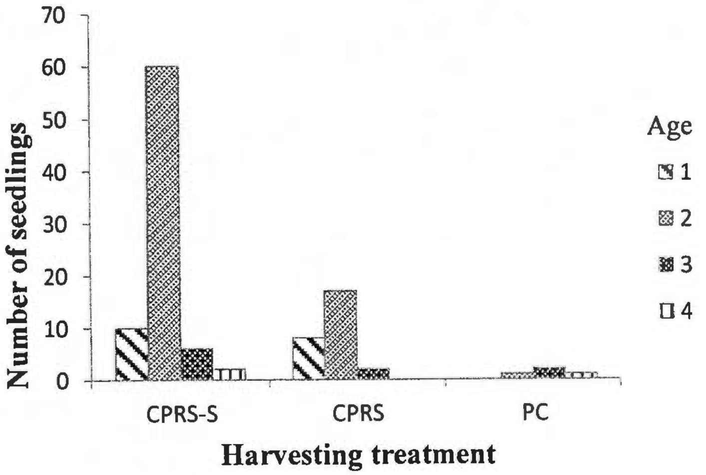

Figure 2.2 Frequency distribution of seedling age for the three harvesting treatments.

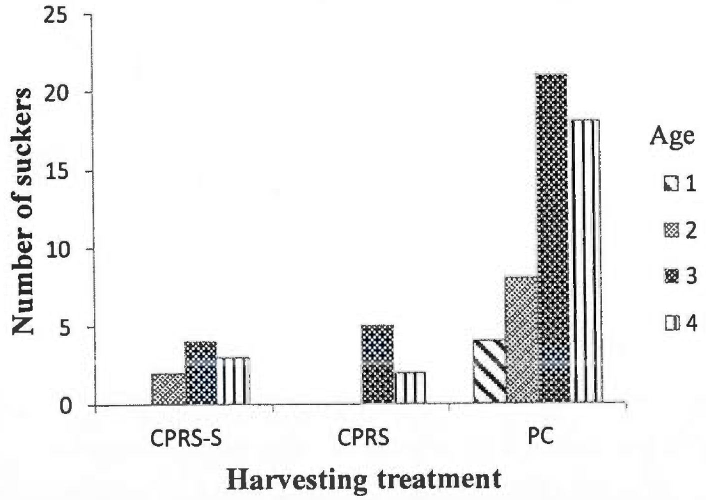

Figure 2.3 Frequency distribution of sucker age for the three harvesting treatments.

The environmental variables (biotic and abiotic) varied between the two sites, and between the three harvesting treatments (Table 2.5). One-way analysis variance showed that the harvesting treatment was a significant factor accounting for the variation in LFH thickness, percentage cover of woody debris and shrubs (Table 2.6). A greater mean LFH thickness was observed in the CPRS-S treatment, while the lowest was found in the PC treatment. The greatest percent cover of woody debris was found in the PC, while there were more shrubs in the CPRS (Table 2.5). Furthermore, the dominant drainage class differed for each harvesting treatment and were moderate, poor, and good for CPRS-S, CPRS, and PC; respectively (Table 2.5) (X^2=225.78 df = 4, p<0.001). We also found significant differences between the two sites for drainage classes (X^2=49.513 df = 2, p<0.001). The dominant drainage class was good and moderate in Authier-Nord and Saint-Dominique, respectively. The application of nonparametric Wilcoxon test revealed significant differences for LFH thickness (W= 9663, p <0.001), and percent cover of shrubs (W= 15808, p<0.001) between the two sites. LFH thickness was lower and the percent cover of shrubs was higher in Authier-Nord compared to St-Dominique.

Table 2.5 Biotic and abiotic environmental factors in each harvesting treatment and site. (*Values are means with SDs given in parentheses)

Site	Harvesting Treatment	LFH Thickness in (cm)	Drainage class (% of the total plots)			% Cover Woody Debris	% Cover Shrubs
			Good	Moderate	Poor		
Saint-Dominique	CPRS-S	19.5(5.2)*		100		12.3(13.3)	21.7(14.9)
	CPRS	22.6(3.4)		5.5	94.5	9.2(5.1)	26.2(19.3)
	PC	17.7(4.4)	58	40	2	24.13(12.0)	15.8(15.1)
	CPRS-S	21.0(5.1)	38	53	9	9.6(5.9)	21.1(13.5)
Authier-Nord	CPRS	14.0(2.9)	24	55	21	16.4(9.6)	29.5(18.9)
	PC	18.6(3.6)	100			15.2(9.7)	33.7(28.3)

Table 2.6 Results of the one-way ANOVA testing the effects of harvesting treatment on LFH thickness, percentage cover of woody debris and shrubs for the three harvesting treatments (CPRS-S, CPRS, and PC).

Response variable	Source	DF	Sum of squares	Mean square	F value	*Pr* > *F*
LFH	Model	2	312	155.98	6.46	0.002**
	Error (within groups)	323	7798	24.14		
% Cover of woody debris [a]	Model	2	24.96	12.48	28.25	<0.001***
	Error (within groups)	323	142.67	0.44		
% Cover of shrubs [a]	Model	2	6.37	3.183	4.04	0.01*
	Error (within groups)	323	254.50	0.79		

Note: [a] Percent cover of woody debris and shrubs were log-transformed

Harvesting treatment (Eq.2.1), LFH thickness (Eq. 2.2), percent cover of shrubs (Eq. 2.3), drainage class (Eq. 2.4) and sites (Eq. 2.5) significantly influenced the density of aspen regeneration *($P<0.05$)*, while the percentage of woody debris had no effect on aspen regeneration density. The harvesting treatments (Eq. 2.1) had the greatest influence on aspen regeneration density but only explained about 13% of the variability in aspen density.

$$E\,(\log(\text{aspen density} + 1) \mid \text{Treatment}) = 0.94 - 0.66(\text{CPRS}) - 0.22\,(\text{PC}) \quad (R^2 = 0.126;\ P < 0.05) \tag{2.1}$$

$$E\,(\log(\text{aspen density} + 1) \mid \text{LFH}) = 1.02 - 0.02\,(\text{LFH}) \quad (R^2 = 0.011;\ P < 0.05) \tag{2.2}$$

$$E\,(\log(\text{aspen density} + 1) \mid \text{Shrub}) = 0.51 + 0.005(\text{Shrub}) \quad (R^2 = 0.015;\ P < 0.05) \tag{2.3}$$

$$E\,(\log(\text{aspen density} + 1) \mid \text{Drainage}) = 0.64 + 0.17\,(\text{D-M}) - 0.32\,(\text{D-P}) \quad (R^2 = 0.05;\ P < 0.05) \tag{2.4}$$

$$E\,(\log(\text{aspen density} + 1) \mid \text{Site}) = 0.41 + 0.46(\text{St-Dominique}) \quad (R^2 = 0.08;\ P < 0.05) \tag{2.5}$$

Aspen regeneration density was nearly five times greater in CPRS-S compared to CPRS, and three times greater in PC compared to CPRS (Eq. 2.1). Aspen density decreased significantly by about 1.5 units (trees ha^{-1}) with each increasing unit of LFH thickness, and increased significantly by about 0.67 units (trees ha^{-1}) with each increasing unit of percent cover of shrubby vegetation (Eq. 2.2 and 2.3). Furthermore, aspen density was greater in the moderate drainage class while it was lower in the poor drainage class *($P < 0.05$)*. Finally, aspen density was nearly three times greater at Saint-Dominique compared to Authier-Nord ($P<0.05$).

All the biotic and abiotic variables significantly explained the presence of aspen seedlings (Table 2.7), but the best predictive model for the presence of aspen seedlings included only the harvesting treatment, based on the AICc values (Table 2.7), according to the following equation;

$$\text{logit } P(\text{presence seedling} \mid \text{treatment}) = 2.16 - 0.81\,(\text{CPRS}) - 4.71\,(\text{PC}) \tag{2.6}$$

The odds ratio for the presence of seedlings was PC<CPRS<CPRS-S, indicating that the probability of finding aspen seedlings was 110 times greater in CPRS-S than in partial cut (Table 2.7).

Table 2.7 Logistic regression coefficients and statistics for models evaluating the impact of disturbance intensity and environmental covariates on the presence of aspen seedlings. (Statistically significant values are given in bold)

Model	Model term	Estimated Value	SE	*z* value	*P*	odds ratio	Δ AIC $_c$	R Nagelkerke (%)
	Intercept	2.16	0.35	6.13	**<0.001**	8.67		
Harvesting treatment	CPRS	-0.81	0.55	-1.46	0.142	3.86	0	48
	PC	-4.71	0.63	-7.5	**<0.001**	0.08		
	Intercept	-0.67	0.28	-2.42	**0.015**	0.51		
Drainage class	Drainage moderate	1.55	0.36	4.30	**<0.001**	2.42	76.38	18
	Drainage poor	3.23	0.78	4.12	**<0.001**	13.0		
LFH thickness	Intercept	-3.13	0.77	-4.06	**<0.001**	1.22		
	LFH	0.19	0.04	4.69	**<0.001**		81.53	15
%Cover woody debris	Intercept	1.39	0.27	5.16	**<0.001**		90.04	11
	woody debris	**-0.06**	**0.02**	-4.12	**<0.001**	1.06		
% Cover shrub	Intercept	0.91	0.25	3.68	<0.001	1.01	105.46	2
	shrub	-0.02	0.01	-2.25	**0.024**			
Site	Intercept	0.90	0.29	3.15	<0.001	1.84	107.39	2
	Saint-D	-0.61	0.34	-1.78	**0.07**			

2.5.2 Aspen genetic and genotypic diversity

All loci were polymorphic (Appendix A) and allelic diversity was high, with a total of 42, 34, and 50 alleles detected in CPRS-S, CPRS, and PC, respectively (Table 2.8). A higher number of alleles were detected at loci 2 (12) and 3 (21) in comparison to the others (loci 1, 4, and 5) Appendix A).

The mean number of alleles per locus was 8.4 ± 1.9, 6.8 ± 1.8, and 10 ± 2.4 in CPRS-S, CPRS, and PC, respectively (Table 2.8). There was a greater number of private alleles in the PC than in the two other treatments (Table 2.8). However, the *G-tests* for allelic frequencies at each locus showed no significant differences in allelic diversity between the three harvesting treatments ($\alpha=0.05$). Mean H_{obs} were 0.54 to 0.56 and 0.48 and H_{exp} were 0.65, 0.64 in CPRS-S, CPRS, and PC, respectively (Table 2.8). Most of the genetic variation was found within rather than between treatments ($F_{ST} = 0.02$ in CPRS-S vs. CPRS; $F_{ST} = 0.007$ in CPRS vs. PC; $F_{ST} = 0.013$ in CPRS-S vs. PC). Genetic diversity parameters were comparable between aspen saplings regenerated by seed or by root suckering, and there was no difference in allelic diversity between the two modes of regeneration (Table 2.9).

Table 2.8 Genetic variability estimates and their mean fixation index (*F*) values between three harvesting treatments. (Standard deviations are given in parentheses)

Diversity parameters	CPRS-S	CPRS	PC
n	49	29	75
N_a	8.4(1.99)	6.8(1.88)	10(2.38)
N_a Freq.>= 5%	3.6(0.6)	4.0(1.05)	4.0(0.84)
N_e	3.9(1.13)	3.64(0.97)	3.96(1.19)
No. private allele	1(0.32)	0.4(0.4)	2.0(0.45)
%P	100	100	100
H_{obs}	0.54	0.56	0.48
H_{exp}	0.65(0.09)	0.64 (0.08)	0.64 (0.09)
F	0.16	0.08	0.25

Note: *n* = sample size; N_a= mean number of alleles per locus; N_a Freq.>= 5%= mean number of alleles with frequency greater than 5%; N_e =mean effective number of alleles per locus; %*P*= percent polymorphic loci; H_{obs}= mean observed heterozygosity; H_{exp}= mean expected heterozygosity.

Table 2.9 Genetic variability estimates and their mean fixation index (*F*) values between seedlings and suckers. (Standard deviations are given in parentheses)

Diversity parameters	Seedlings	Suckers
N	63	40
N_a	9.2(2.17)	8.2(2.13)
N_a Freq.>= 5%	3.8(0.73)	4.0(0.84)
N_e	3.9(1.0)	3.7(1.15)
I	1.5(0.25)	1.4(0.31)
Nb. private alleles	2.2(0.37)	1.2(0.37)
%P	100	100
H_{obs}	0.56	0.41
H_{exp}	0.66(0.07)	0.6(0.11)

Note: *n* = sample size; N_a= mean number of alleles per locus; N_a Freq.>= 5%= mean number of alleles with frequency greater than 5%; N_e= mean effective number of alleles per locus; *I*= information index; %*P*= percent polymorphic loci; H_{obs}= mean observed heterozygosity; H_{exp}= mean expected heterozygosity.

A total of 137 putative multilocus genotypes were identified out of 153 samples analyzed. Clonal diversity (*G/N*) was high and similar for all of treatments: 0.93, 0.89, and 0.87 in CPRS, PC, and CPRS-S, respectively (Table 2.10). The proportion of clones consisting of only one ramet was 95% in CPRS-S, 93% in CPRS and 91% in PC. The largest clone consisted of 5 ramets and was found in the CPRS-S treatment. Mean genotypic diversity was very high (*G/N=0.9)* in sucker-regenerated aspen with 88% of the genets represented by a single ramet.

Table 2.10 Summary of clonal diversity for the three harvesting treatments for the five loci.

Treatment	Sample size	Genets	Multiramet genets	Single ramet genets	G/N
CPRS-S	49	43	2	41	0.87
CPRS	29	27	2	25	0.93
PC	75	67	6	61	0.89

Note: N= Number of multi-and single-ramet genets, G/N= multilocus genotypic diversity.

2.6 Discussion

Our results showed that disturbance intensity had a significant impact on the mode and density of aspen regeneration, but do not support our initial predictions that a greater disturbance intensity (CPRS-S) would increase aspen density compared to a low disturbance intensity (PC).Recruitment from seedlings was the main mode of aspen regeneration in the CPRS-S and CPRS treatments. CPRS-S and CPRS treatments allow more seedlings establishment because the scarification process (in CPRS-S) and machinery traffic expose bare mineral soil (Zasada *et al.*, 1983; Lavender *et al.*, 1990; Prevost, 1996, 1997; Romme *et al.*, 2005). All recorded environmental variables except for the percent cover of woody debris had an effect on aspen regeneration density and mode of regeneration, however these effects only explained very little variation. It thus seems that other environmental variables are more important. Surprisingly we detected that LFH thickness had a positive influence on the presence aspen seedlings, observing 1.22 times more aspen seedlings with the increase in LFH thickness of one unit (Table 2.7). However, there was a very large variance in in mean LFH thickness within each treatments, and it is likely that establishment of the treatment blocks may have been biased by the machinery operators, who preferentially chose to scarify wetter patches with more organic matter accumulation. This could explain why we found greater LFH thicknesses in the CPRS-S treatments, even after scarification.

Most of the seedlings emergence occurred within two years after cutting (after scarification) and this successful establishment of aspen seedlings can be explained by the presence of adequate moisture and the elimination of competing vegetation during the germination period (Figure 2.2). We also showed that the presence of seedling decreased with increasing the percent cover of shrubs (Table 2.7). In many cases after a clear-cutting, vegetation is composed of very competitive species (e.g., *Carex geyeri, Calamagrostis rubescens, Epilobium angustifolium, etc.* (Lieffers & Stadt, 1994; Riegel *et al.*, 1995), making seedling establishment difficult or even impossible.

We predicted that root suckering would produce greater densities of aspen and would be the main mode of regeneration in CPRS and CPRS-S, based on the fact that complete canopy opening and increased soil temperatures are reputed to stimulate aspen root suckering

(Peterson & Peterson, 1992; Zasada & Packee, 1995, Chen & Popadiok, 2002). The low number of suckers found in CPRS-S and CPRS are probably due to factors associated with the pre-harvest conditions. Root suckering requires the presence of roots in pre-harvest stands (Shepperd *et al.*, 2001; Frey *et al.*, 2003; Jones *et al.*, 2005), which suggests that the studied CPRS and CPRS-S plots had much less aspen stems in the pre-harvest stand compared to the PC blocks. Since the data we had on pre-harvest conditions only included aspen density as a whole for each site not specifically for each block corresponding to the harvesting treatments (Table 2.1), we cannot assess pre-harvest stands conditions into each treatment plots besides counting the number of aspen stumps. We found 7, 13 and 28 aspen stumps on average in CPRS, CPRS-S, and PC for both sites, respectively (data not shown); we can conclude that aspen density in post-harvest stands was probably more related to the presence of aspen trees in the pre-harvest stands rather than to specific harvesting treatments (Table 2.7).

It is also possible that some of the first-established suckers did not survive in the CPRS-S treatments (Figure 2.3); as noted by Prevost and Pothier (2003) scarification could have amplified first-year suckering, but reduced growth and survival of the suckers for the following years. Other authors reported high sucker mortality (Bates *et al.*, 1993), and reductions in sucker densities and height (Smidt & Blinn, 2002; Stone & Kabzems, 2002) with scarification. This could be due to breakages of the parental root system by the scarifying disks, on which the suckers are highly dependent for their initial growth and survival (Zahner & Debyle, 1965).

It was nevertheless surprising to find high aspen densities in the PC treatment considering that this treatment limits environmental changes between pre- and post-harvest conditions and that some stems are left intact and continue to transfer auxins into the communal root system to inhibit root suckering (Prévost & Pothier, 2003). Clearly our results do not support the idea of using partial cutting to inhibit aspen suckering (Gifford, 1967; Huffman *et al.*, 1999; Puettmann *et al.*, 2008).

2.6.1 Genetic structure

This work is the first to study the mode of aspen recruitment in coniferous dominated stands through dendrochronological analysis in combination with molecular analysis to identify and characterize genetic and genotypic structures of invading aspen. Studies of aspen diversity show high levels of genetic variation, indicating that aspen is not only one of the most widely distributed hardwood species but also one of the most genetically diverse species (Stevens *et al.*, 1999; Wyman *et al.*, 2003). High genetic diversity parameters (Table 2.8) demonstrated that the five microsatellite markers used in this study provided sufficient strength to identify high number of alleles and to reveal no significant difference in allelic diversity between the three harvesting treatments. The dynamics of genetic and genotypic diversity was high between the three harvesting treatments. The high levels of polymorphism (100%) observed in the new aspen established are comparable with values reported in several studies (Ellstrand & Roose, 1987; Liu & Furnier, 1993; Wyman *et al.*, 2003; Namroud *et al.*, 2005). Averaged across loci, the total number of alleles per locus varied between 8.4, 6.8, and 10 in the three levels of disturbances (Table 2.8; refer to Appendix B), and were comparable to previous studies (Wyman *et al.*, 2003; Namroud *et al.*, 2005). This value is higher than that found for the four loci among aspen individuals from Alberta, from which they were initially identified (Dayanandan *et al.*, 1998), or for an additional seven loci (Rahman *et al.*, 2000) where there were 3.7 alleles per locus. It has been generally assumed that genetic diversity should increase with the greater chance of presence aspen seedlings (Jelinski & Cheliak, 1992). However, our results showed that there was high genetic diversity with either seedling or sucker recruitment (Table 2.9).

We found higher levels of both observed and expected heterozygosities, H_{obs} ranging from 0.48 to 0.56 and H_{exp} ranging from 0.64 to 0.65. The level of expected heterozygosity, also a measure of genetic variation, in the current study was high in all three harvesting treatments (Table 2.8). This was similar to those values found by Wyman *et al.*, (2003) and Namroud *et al.*, (2005) in studies conducted in Quebec. However, it exceeds two or three times in comparing with other studies that used isozymes (Jelinksi & Cheliak 1992; Stevens *et al.*, 1999). The high rates of heterozygosity in this study have been attributed to greater chances of aspen seedling recruitment or suckering of different and intermingled genotypes. Likewise, the greatest genetic variation in all three harvesting treatments was distributed within rather than among them, as evidence by the F_{ST} (Table 2.8), suggesting a very different stand make up in the eastern forests versus western forests (Wyman *et al.*, 2003; Hipkins & Kitzmiller, 2004).

Genotypic diversity was high among the samples and no significant difference in genotypic diversity was observed between the three harvesting treatments (Table 2.10). This result was comparable to (Wyman *et al.*, 2003; Namroud *et al.*, 2005; Jelinkova *et al.*, 2009) that reported high *G/N* values for the northwestern Quebec boreal forest. The high number of genotypes sampled was quite high, indicating the presence of many small clones. The high levels of genotypic diversity and the large number of genets made of only one ramet indicated multi-clonal stand structures. One would expect that clone size and genotypic diversity would be explained through the different modes of aspen recruitment (sexual *vs* asexual). Therefore, the lack of difference in genetic and genotypic diversity between the two modes of regeneration raises questions. It seems that high clonal diversity is more reliant on greater frequency of successful seedling events (Jelinski & Cheliak, 1992; Mitton & Grant, 1996). Our results confirmed this pattern as we found a lot of aspen seedlings despite the supposed rarity of seedlings recruitment in aspen (Latva-Karjanmaa *et al.*, 2003). Moreover, in the recent studies in western North America, microsatellite data found a surprisingly large number of distinct genets that were represented by only one to a few individual ramets, and also concluded the recent sexual recruitment presented a stronger contributor to genetic variation (Mock *et al.*, 2008). The high aspen clonal diversity found in PC treatment, despite its vegetative regeneration through root suckering, demonstrates it does not merely relate to the mode of aspen recruitment. Suckers from different genotypes are likely to be highly intermixed after a large suckering event (Steneker, 1973) causing frequent chances of vegetative reproduction from different genotypes. Since high genetic diversity and a large number of unique genets were present in all three levels of disturbance intensity (CPRS-S, CPRS, and PC) either seedlings or suckers, we deduce that the three levels of disturbance intensity originated from a common and diverse genetic pool that was established at the origin of the stands.

2.7 Conclusion

In summary, results from our study indicate that the harvesting treatments, biotic and abiotic conditions measured in this study, even though they were statistically significant, were inefficient in predicting aspen density and mode of regeneration into coniferous stands. However, our results showed well that harvesting created conditions, either in severe or light disturbance intensities that allowed the invasion of aspen into black spruce forests. Our results also highlight the need to consider aspen density in pre-harvest stands.

A considerable number of aspen were recruited through seedlings in CPRS-S, and CPRS, while the majority of aspen are recruited through suckering in the PC. This shows that aspen establishment from seed is more frequent than previously thought in post-harvest stands. However, recent studies have explained that aspen stands contain much more genetic diversity than once assumed (Mock *et al.* 2008, DeWoody *et al.* 2009), and numerous aspen seedlings have been found after disturbance in recent years (Turner *et al.* 2003, Landhäusser *et al.* 2010), indicating that seedling establishment may be more common than once thought.

It can be expected that aspen will become more frequent in the future, as harvesting and natural disturbances are becoming more frequent in northwestern Quebec and northeastern Ontario (Harvey & Bergeron, 1989; Bergeron *et al.*, 2004; Laquerre *et al.*, 2011). Finally, high clonal diversity was maintained in all types harvesting treatments, with either seedling establishment or suckering of many different clones.

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CHAPTER III

GENERAL CONCULSION

This study documented aspen recruitment (aspen expansion) after harvesting into conifer-dominated stands of northwestern Quebec boreal forest. Our results are consistent with reports from northwestern Quebec and northeastern Ontario (e.g. Carleton & MacLellan, 1994; Carleton, 2000; Grondin *et al.,* 2003; Laquerre *et al.*, 2009, 2011) showing aspen's northern expansion into the black spruce forest. Our study also clearly showed that aspen recruitment through seedling establishment is more frequent than previously expected (Perala, 1990; Jelinski & Cheliak, 1992; Greene *et al.,* 2007). We predicted that sexual reproduction would be infrequent because aspen seeds are very short lived and seedbed conditions suitable for germination are quite narrow and uncommon in areas where mineral soil exposure is not prevalent (David *et al.,* 2001). However, previous research at the Northern Forestry Centre in Alberta has revealed an abundance of seedlings, primarily in lodgepole pine cutovers on mesic and subhydric sites (Peterson & Peterson, 1992), at variable densities (ranging from 1,000 to 16,000 seedlings per hectare). Other reports of seedling establishment following disturbance into higher elevation of the Rocky Mountains questions the notion that exposure of mineral soil substrate in conjunction with a warming climate plays a main role in aspen seedlings establishment (Landhäusser *et al.*, 2010).

Many seedlings established rapidly after harvesting in our CPRS-S and CPRS treatments at different densities. The wide canopy opening and exposure of mineral soil resulting from the machinery traffic and soil scarification, combined with good moisture availability in our sites provided suitable conditions for seed germination and establishment of aspen seedlings. This result was surprising considering that our CPRS-S and CPRS blocks had on average greater thicknesses of organic layer. Scarification of patches with thick organic layers to favour early establishment of natural and planted conifer seedling has thus also favored the establishment of aspen seedlings. However, the difference in aspen seedlings density between the two harvesting treatments indicated that site drainage could also play a significant role in aspen recruitment. The best chances for seed emergence and survival are often observed on a mineral soil that is continually moist, well-drained and free of competition (Steneker, 1976).

The drainage conditions in our CPRS-S blocks had suitable conditions for the emergence of seedlings in comparison to our CPRS blocks. We did not expect successful aspen seedling establishment in the PC treatment due to low light availability created by partial canopy opening. Aspen is a pioneer species that is less able to maintain a positive net photosynthesis rate at low light (Messier *et al.*, 1999). Our results showed that the PC treatment limited aspen seedling recruitment but did not inhibit suckering.

Even though we found significant differences in aspen density between the three harvesting treatments, the low R^2 associated with our models indicate that our recorded environmental variables (LFH thickness, Drainage class, and percentage cover of shrubs) were poor predictors of post-harvest aspen density. It thus appears that pre-harvest site characteristics, especially the presence of aspen, had more influence on post-harvest aspen recruitment. The number of suckers that arise following a disturbance is dependent upon the number and density of roots that exist in the pre-harvest stand (Shepperd *et al.*, 2001). In PC treatment, forestry operators are usually instructed to remove aspen in priority and leave spruce trees in order to limit light penetration into the post-harvest stands. This has for consequence to break off apical dominance in the aspen roots, on top of the possible increase in soil temperatures caused by canopy opening, both triggering suckering (Maini & Horton, 1966).

The increase in light intensity due to canopy opening also influences aspen suckering (Prévost & Pothier, 2003). In a previous study aspen sucker regeneration density was shown to increase from 28,751 stems ha^{-1} in the one-third to 63,333 in two-thirds harvesting treatments and 102,916 stems ha^{-1} in the clear-cut in northwestern Quebec (Brais *et al.*, 2004). Therefore, it is probable the light transmitted in the PC treatment was higher than the light intensity threshold that could limit aspen invasion. Our hypothesis that aspen establishment would increase with the level of disturbance thus needs further investigation, especially in regards to the pre-harvest conditions and the light dynamics in stands. We couldn't conclude on the basis of our own results which factors might have more influence on controlling aspen invasion into coniferous forests.

3.1 Aspen genetics

The type of harvesting treatments did not show any significant differences on aspen genetic and genotypic diversities. Indeed, there was great genetic and genotypic diversity in all levels of harvesting. This is consistent with previous studies that showed that aspen stands in northwestern Quebec have great genotypic diversity with the presence of many small clones (Wyman *et al.*, 2003; Namroud *et al.*, 2005). More interestingly, we showed that clonal diversity was maintained with both modes of aspen recruitment (sexual and vegetative), even though we expected that genotypic diversity would be higher for seed-regenerated aspen compared to sucker-regenerated aspen. A loss of genotypic diversity is expected with vegetative regeneration, because all new sprouts (suckers) from the parent tree's root system have the same genetic makeup as the parent tree. The high level of genotypic diversity in aspen indicates a highly diverse genetic pool existing in Quebec's boreal forests. This could be explained by a high probability of sexual reproduction.

It should be noted that harvesting practices can significantly impact genetic variability in regenerated forest population (Rajora, 1999). In this respect, an understanding of the impact of various harvesting methods on gene pools will facilitate the monitoring of these practices to ensure their effectiveness in maintaining long term ecosystem sustainability and genetic integrity (Mosseler & Rajora, 1998). Therefore, a better understanding of the genetic variability and clonal structure between pre and post-harvest can provide insights into aspen genetic dynamics and may provide information on potential responses of aspen in coniferous dominated stands to different methods of harvesting. From this perspective, sampling the pre and post-harvest stands in each treatment and comparing their genetic structure would probably give us better chances of discovering aspen genetic dynamics.

3.2 Management implications

There is no doubt that boreal forests are currently dominated by pioneer-species and are more spatially heterogeneous than has been previously thought (Cumming *et al.* 2000). This research supports the observations widely reported in the literature that aspen is expanding into coniferous forests of eastern Canada. The conversion of coniferous forests into mixed or broadleaved forests by our current harvesting practices raises concerns for forest managers. Our study creates evidence that disturbances such as CPRS-S, CPRS, and PC increase the proportion of aspen into mainly coniferous stands of northwestern Quebec. Unfortunately, our study brought little elements to explain aspen recruitment into post-harvest coniferous based on different disturbances intensities. Since we found much seed regeneration in the CPRS and CPRS-S treatments, it seems that aspen invasion in these treatments, even with thick organic layer thicknesses, is inevitable. In the PC treatment, because most aspen were of sucker-origin, the factor controlling aspen recruitment was the presence of a pre-established root system. In that case, perhaps partial harvesting without removing the aspen stems would limit suckering by maintaining apical dominance (hormonal ratios, see general introduction) in the root network. However this defeats the purpose of leaving more space for the conifers to grow with partial harvesting.

We believe that the disturbance intensity played a certain role in enhancing aspen recruitment although there were other factors at play. Indeed, disturbance intensity should be adapted to overstory composition. As an example, in boreal Quebec light levels are higher under shade-intolerant species such as aspen and *Pinus* than under shade-tolerant conifers (Messier *et al.*, 1998). Thus, in conifer-dominated stands, heavier cutting is required to promote growth of conifer advanced regeneration, assuming hardwood competitors are controlled. Drawing the future stand composition based on the current stand structure must however be done cautiously, because future growing conditions may not be optimal for aspen (thick organic layers in CPRS and CPRS-S and understory light conditions for PC). In this respect, others have found that partial cutting with leaving a residual over-story in western Canadian boreal mixedwood stands suppressed hardwood regeneration and favoured associated conifers (Man & Lieffers, 1999), but this approach may not be as effective in eastern Canadian stands (MacDonald *et al.*, 2004). On the other hand, the PC method may not be economically feasible because initial harvest volumes are less and access roads require maintenance to allow the future removal of residual trees.

The concept of emulating natural disturbance has emerged in forestry as a management strategy that seeks to maintain economic value from clear cutting while sustaining the structure and composition of stands. In this respect, forest management based on emulation of natural disturbances requires an increased knowledge of aspen dynamics and genetic structure at different seral successional stages. There has also been recognition that succession towards mixed or conifer-dominated stands is variable and related to the rate of which hardwood stands are invaded by coniferous species (Galipeau *et al.*, 1997). In this regard, Bergeron and Harvey (1997) expressed a silvicultural method based on the successional pattern. This system permits forest managers to favour the transition of aspen stands towards mixed or coniferous stands. As a consequence, a clear understanding of which methods seem to be the most efficient for controlling aspen invasion must be considered from the initial characteristics of the stands. Further studies are required to investigate the effects of other factors on aspen dynamics, such as season of harvest, soil temperature, and aspen density in pre-harvest stands.

APPENDIX A: Allele frequencies of aspen per locus and per treatment in post-harvest between harvesting treatment.

Locus	*CPRS-S*	*CPRS*	*PC*
Locus1			
238	0.01	0.276	0.147
247			0.027
250	0.765	0.690	0.713
253			0.007
259	0.051	0.034	0.02
262	0.02		0.013
265	0.133		0.047
268	0.02		0.027
Locus 2			
195	0.010		0.007
198	0.010		
201	0.041		0.007
204	0.031	0.207	0.147
207	0.235	0.172	0.233
208			0.013
210	0.092	0.138	0.120
213	0.214	0.259	0.213
216	0.143	0.138	0.100
219	0.163	0.086	0.12
222	0.041		0.04
228	0.02		
Locus 3			
184	0.01	0.052	0.033
212	0.031	0.017	0.02
213			0.007
214	0.02	0.017	0.060
216		0.017	0.013
218	0.01		0.020
220		0.017	0.027
222	0.01		0.013
223			0.007
224	0.204	0.241	0.16
226	0.163	0.103	0.127
228		0.034	0.02
230	0.102	0.052	
231	0.01		
232	0.173	0.259	0.260
234	0.163	0.069	0.1
236	0.01	0.034	0.08
238	0.01	0.034	0.007
240	0.041	0.052	0.02

Continued…

Locus	*CPRS-S*	*CPRS*	*PC*
Locus3			
241			0.007
242	0.041		0.02
Locus 4			
198	0.531	0.603	0.553
200	0.429	0.310	0.3
204			0.007
206	0.02	0.017	0.033
216	0.01		
218		0.034	0.04
220	0.01	0.034	0.053
224			0.007
226			0.007
Locus 5			
132	0.02	0.017	0.033
134	0.02		
136	0.163	0.155	0.067
138	0.561	0.621	0.727
140	0.235	0.155	0.16
142		0.017	
146		0.034	
148			0.013
150			

APPENDIX B: Observed and expected heterozygosity per locus in each harvesting treatment. H_{obs}=observed heterozygosity; H_{exp}= expected heterozygosity; numbers between parentheses indicate the standard variations of heterozygosity; F is information index; *P* is the probability that allele frequencies at a specific locus are in Hardy-Weinberg equilibrium.

	CPRS-S				CPRS				PC			
Allele /locus	H_{obs}	H_{exp}	F	*P*	H_{obs}	H_{exp}	F	*P*	H_{obs}	H_{exp}	F	*P*
Locus 1	0.38	0.39	0.01	ns	0.62	0.45	-0.4	ns	0.49	0.46	-0.06	***
Locus 2	0.81	0.84	0.02	ns	0.83	0.81	-.01	*	0.63	0.84	0.2	***
Locus 3	0.81	0.86	0.05	***	0.55	0.85	0.3	***	0.59	0.86	0.3	***
Locus 4	0.51	0.53	0.04	ns	0.65	0.54	-0.2	ns	0.56	0.59	0.06	***
Locus 5	0.18	0.60	0.7	***	0.17	0.56	0.7	***	0.13	0.44	0.7	***
Average gene diversity	0.54 (0.1)	0.65 (0.09)			0.56 (0.1)	0.64 (0.1)			0.48 (0.09)	0.64 (0.09)		

Mean H_{obs} / H_{exp} = 0.53/0.64

Note: ns=not significant; * *P<0.05*, ** *P<0.01*, *** *P<0.001*

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