UNIVERSITÉ DU QUÉBEC À MONTRÉAL

THE ROLE OF SPATIALLY AGGREGATED POST-HARVEST WOODY RESIDUE IN SOIL FERTILITY AND THE ESTABLISHMENT, GROWTH, AND FLOWERING OF PLANTS

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DEDICATION

To the learning, understanding and enjoyment
of life through science and culture

FOREWARD

This dissertation is composed of a global introduction, three research chapters, and a global conclusion. Each chapter is written in a standard scientific journal format with an introduction, methods, results, and discussion sections. The literature cited in each chapter is found at the end of the dissertation. I was responsible for the field and lab research, and the hypotheses, development and writing of each chapter.

The first chapter, *The role of aggregated forest harvest residue in soil fertility, plant growth, and pollination services*, has been published as McCavour, M.J., Paré, D., Messier, C., Thiffault, N., and Thiffault, E. 2014. The role of aggregated forest harvest residue in soil fertility, plant growth, and pollination services. Soil Science Society of America Journal 78:196-S207. The co-authors are members of my proposal committee. I was responsible for developing the ideas, methodology, conducting the field and lab work, writing the draft and final version. My supervisors helped with laboratory methodology and suggestions at all stages.

The second chapter, not yet submitted for publication, is titled *The effect of proximity to aggregated slash on the growth of hybrid poplars*. I was responsible for developing the ideas, methodology, conducting the field and lab work, and writing the draft and final version. My supervisors helped with laboratory methodology and suggestions at all stages.

The third chapter is titled *Forest harvest residue loading and the juvenile survivorship of small-seeded tree species*. It has also not yet been submitted. I was responsible for developing the ideas, methodology, conducting the field and lab work, writing the draft and final version. My supervisors helped with laboratory methodology and suggestions at all stages.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

RÉSUMÉ

Cette thèse porte sur les avantages de la rétention d'empilement de résidus de bois après coupe, pour la biodiversité et la production de biomasse, par l'augmentation de la fertilité des sols, la croissance et la floraison. Cette recherche a pour contexte de maintenir la production forestière et des services écosystémiques des plantations industrielles, tout en maximisant l'étendue des terres forestières naturelles et en respectant les compromis à la fois écologiques et économiques de la rétention des résidus forestiers à travers les changements climatiques et des conditions économiques. Le projet examine, en particulier, les effets de l'empilement de résidus forestiers sur la fertilité des sols, la croissance des peupliers hybrides et d'espèces de plantes non-commerciales, l'abondance des ressources pour les pollinisateurs et les frugivores, et l'établissement de plusieurs espèces de semences. Un thème important est que la rétention d'empilement de résidus forestiers après coupe, parce qu'elle favorise et retarde l'abondance de beaucoup d'espèces, peut être considérée comme un outil de gestion durable des forêts pour être utilisée à des fins diverses, plutôt que d'être seulement vu comme une accumulation de biomasse dangereuse pouvant alimenter les feux de forêts ou une opportunité commerciale pour le marché de la bioénergie.

Le chapitre 1 démontre que la fertilité du sol diminue avec la distance à partir des empilements de résidus sur les sites sablonneux de la Rivière-aux-Rats (RAR) au Québec. La baisse exponentielle de l'azote et du phosphore disponibles en fonction de la distance se stabilise à environ 10 m des résidus forestiers. Il est démontré qu'une corrélation positive existe entre la croissance, la production de fleurs et de fruits avec trois plantes fruitières communes (i.e., cerisiers de Pennsylvanie, fraisiers et framboisiers) en fonction de la disponibilité des nutriments; i.e., ces mesures sont inversement corrélées avec la distance à partir des résidus forestiers jusqu'à 10 m plus loin. Il est entendu que l'empilement de résidus plus volumineux se trouvant dans un paysage forestier industriel peut avoir une grande importance au niveau du maintien, non seulement pour les espèces en début de succession, mais aussi des populations de pollinisateurs et frugivores qui en dépendent.

Le chapitre 2 est basé sur le même jeu de données (i.e., des empilements de résidus forestiers du site à la Rivières-aux-Rats) mais se concentre sur la croissance des peupliers hybrides plantés. Comme avec les plantes à fleurs entomophiles, les peupliers montrent une baisse de croissance exponentielle selon la distance à partir des résidus forestiers allant jusqu'à environ 10m plus loin. Proche des résidus, les arbres avaient de

plus grandes quantités de cations foliaires et un meilleur accès aux éléments nutritifs du sol par rapport aux arbres plus éloignés de ces mêmes résidus forestiers. C'est à partir de la troisième année après coupe que le taux de croissance des peupliers près des résidus, a commencé à augmenter par rapport aux tiges qui étaient plus éloignées de ces résidus. La loi de rendement final constant est utilisée pour montrer que l'amélioration de la croissance doit être dues aux ressources supplémentaires ; en effet, il a été calculé que les peupliers près des résidus doivent avoir environ un apport en éléments nutritifs doublé comparativement aux tiges plus éloignées des résidus. Il a été conclu que l'empilement des résidus forestiers peut réduire le temps de rotation de coupe, et ce, devrait être considéré si l'un calcule la valeur attribuée au prélèvement de la biomasse utilisée à des fins de biocarburants.

Le chapitre 3 examine la phase précoce d'établissement du recrutement sexuel de différentes semences d'espèces d'arbre. L'étude a été conduite près des mêmes sites de la Rivière-aux-Rats, encore une fois sur un sol sablonneux. Dans une coupe à blanc âgée d'un mois, nous avons regroupé et classé des résidus selon la taille à partir d'un volumineux amoncellement de résidus forestiers pour créer de plus petits agrégats de ceux-ci, de 1x1 m variant entre 0 et 60 kg/m2 (variation de charge typique que l'on retrouve à une petite échelle parmi et à l'intérieur des blocs de coupe). À l'intérieur de chaque empilement nous avons semé des graines de bouleau jaune et d'épinette blanche, en ayant comme prémisse que le taux de survie augmenterait selon la charge de l'empilement due à l'optimisation de la rétention d'eau jusqu'à un maximum puis ensuite diminuer à mesure que (1) le piégeage des graines empêcherait le contact avec le substrat minéral et (2) l'ombrage croissant conduirait à la mortalité des semences. Les deux espèces ont montré une réponse similaire, avec une survie maximale se produisant de 4 (bouleau) ou 8 (épinette) kg/m2. Globalement, l'étendue optimale pour l'établissement de semis chez les deux espèces, était lorsque les charges des résidus pesaient entre 2-12 kg/m2, ce qui est assez similaire à l'étendue des valeurs moyennes se rapportant suite à une récolte "cut-to-legth".

Les résultats de cette thèse sont novateurs. Par exemple, aucune étude auparavant a utilisé un gradient de distance pour examiner la fertilité des sols par rapport à la proximité des empilements de résidus forestiers, ni utilisé de gradient afin de déterminer la charge optimale de l'empilement de résidus pour l'établissement des semis (découvrant simultanément une source majeure d'une grande variation de la survie retrouvée dans la littérature relié à l'établissement de semis). De même, cette étude est la première à signaler le rôle qu'a la proximité de l'empilement de résidus forestiers avec la floraison et la fructification des espèces végétales de début de succession et, à leur tour, leur rôle en procurant des ressources alimentaires pour la faune. L'utilisation de la loi de rendement croissant pour examiner la croissance des arbres en plantations et de différencier les effets de la disponibilité des nutriments et de la compétition souterraine est une approche novatrice pour aborder la question, qui est

de savoir si les résidus forestiers doivent être utilisées comme source d'énergie maintenant ou plus tard, dans une usine (en plus de la biomasse des arbres récoltés ou d'une rotation de récolte raccourcie).

Il est maintenant évident que l'empilement de résidus forestiers est profitable pour un grand nombre d'espèces, y compris les plantations. Ainsi, ce travail devient une contribution à ce débat en constante évolution sur la façon dont les résidus forestiers après coupe devraient être utilisés et de mieux calculer le coût net en retirant ces résidus forestiers pour soit les biocarburants ou pour réduire les risques d'incendie. Enfin, cette thèse illustre l'utilité à considérer la rétention des résidus forestiers et leur retrait comme un outil flexible à usages multiples de gestion durable des forêts.

Mots clés : *résidus après coupe, fertilité des sols, gestion de feux, pollinisateurs, loi de rendement final constant, peupliers hybrides, services écosystémiques, coupe à blanc, biodiversité.*

ABSTRACT

This dissertation focuses on the benefits of retention of piled post-harvest slash to biodiversity and biomass production, through increased soil fertility, growth, and flowering. This research is within the context of sustaining forest production and ecosystem services of industrial plantations while maximizing the extent of natural forestlands, and with respect to the ecological and economic trade-offs of slash retention under changing climate and economic conditions. In particular, the project examines the effects of aggregated slash on soil fertility, the growth of hybrid poplar and non-commercial plant species, the abundance of resources for pollinators and frugivores, and the establishment of small-seeded species. A major theme is that retention of post-harvest residue, because it promotes and retards the abundance and diversity of species, can be regarded as a sustainable forest management tool to be used for various ends, rather than seen only as a dangerous accrual of fuel for fire or a commercial opportunity for the bioenergy market.

Chapter 1 begins by demonstrating that soil fertility decreases with distance from slash piles on sandy sites at Riviere-aux-Rats (RaR) in Quebec. The exponential decline in available nitrogen and phosphorus with distance flattens at about 10 m. It is then shown that three common fruiting plants (pin cherry, strawberry, and raspberry) have growth, flower production and fruit production positively correlated with nutrient availability; i.e. these measures are inversely correlated with distance from pile out to 10 m. It is concluded that large aggregations of residue in an industrial forested landscape may be very important in the maintenance not only of early successional plant species, but also of the populations of pollinators and frugivores dependent upon them.

Chapter 2 is based on the same set of piles at RaR but is focused on the growth of planted hybrid poplars. As with the entomophilous flowering plants, the poplars show an exponential decline in growth with distance from pile to about 10 m. Near-pile trees had larger amounts of foliar cations and greater access to soil nutrients relative to trees far from piles. The growth rates of the poplars near the piles began to accelerate relative to far-pile stems starting in the third year post harvest. The theory of constant final yield is used to show that the enhanced growth must be due to added resources; indeed, it is calculated that poplars near piles must have about double the nutrient availability as stems far from piles. It is concluded that aggregated slash retained on-site can reduce rotation time, and this should be considered as one calculates the value of its removal for biofuel.

Chapter 3 examines the early establishment phase of sexually recruiting small-seeded tree species. This was near the same RaR site, again on a sandy soil. In a one-month old clearcut we gathered and size-classed slash from a large pile to create 1x1 m slash aggregations varying in loading from 0 to 60 kg/m^2 (typical of the range found at a small scale among and within harvest blocks). In each pile we sowed seeds of yellow birch and white spruce, hypothesizing that survivorship would rise with loading due to improved water retention up to a maximum and then decline as (1) the trapping of seeds precluded contact with the mineral or duff substrate, and (2) the increasing shade led to germinant mortality. The two species showed a similar response, with a maximum survivorship occurring at 4 (birch) or 8 (spruce) kg/m^2. Broadly, the optimal range for seedling establishments for either species was for loadings between 2-12 kg/m^2, which is quite similar to the range of mean values reported following cut-to-length harvesting.

The results of this dissertation are novel. For example, no study previously has used a fine distance gradient to examine soil fertility in relation to slash pile proximity, nor used a gradient to determine optimal loading for seedling establishment (simultaneously uncovering a major source of the large survivorship variation found in the seedling establishment literature). Likewise, this is the first study to report the role of slash pile proximity in the flowering and fruiting of early successional plant species and, in turn, their role in the provision of food resources for wildlife. The use of the law of constant yield to examine the growth of crop trees and differentiate the effects of nutrient availability and below ground competition is a novel approach to addressing the question of whether slash should be used as a source of energy in a mill now, or later (expressed on nutrient poor sites as additional harvested tree biomass or as shortened rotation time).

It is clear that aggregated slash, through its nutrient release or provision of habitat or shelter, can benefit a large number of species including crop plants. Thus this work becomes a contribution to the evolving debate on how to use post-harvest residue and better calculate the net cost of removing slash for biofuel or for fire hazard reduction. Finally, it illustrates the utility of viewing slash retention and removal as a flexible multi-goal sustainable forest management tool.

Keywords: *post-harvest residue, soil fertility, slash, fuel management, pollinators, law of constant final yield , hybrid poplar, clearcut, ecosystem services, biodiversity*

GLOBAL INTRODUCTION

Introduction

During the last 40 years, the study of dead wood has been driven by three concerns. The first was in the 1970s and 1980s when the progenitors of the "New Forestry" (Gillis 1990) began to point out a problem associated with bole removal during clearcuts: there was a large number of species dependent upon deadwood as habitat for nesting, feeding, or germination. The second wave of interest started perhaps two decades later as concern for global warming led to a renewed concern with rates of carbon storage and loss within forests (Dixon et al. 1994). A third, more recent, focus has been occasioned by increasing energy prices, leading many governments and forestry companies, especially in Scandinavia, to begin using forest harvest residue for energy generation (Lattimore et al. 2009).

During most of the preceding century, post-harvest residue (slash) was regarded as an unfortunate waste or bi-product of bole removal. With the mechanization of forest harvesting operations, it became more practical to remove branches at the roadside (that is, whole tree harvesting). Instability of delimbing machinery on uneven ground within the cut-block, efficiency, and the safety of workers were the main imperatives driving this change (Davis et al., 2001).

One negative aspect of slash was that it impeded the movement of equipment and planters; another is that it restricted the planting area. Therefore, it was typically piled at the landing following whole-tree harvesting and often-times burned simply to remove it.

A second reason to burn residue at the landing was that slash, where well-aggregated, increases the fire hazard (Fernandes and Notelho, 2003). This is an issue that has become increasingly important as many western forests in the United States and Canada transition from discontinuous to continuous canopy cover (due to successful fire suppression), and thus a stand-replacing fire regime replaces what were traditionally ground-fire regimes (Miller et al., 2012) on the lower slopes of Western mountains. Thus slash removal is seen as an effort to reduce fire intensity.

There is an emerging third reason to remove slash from a cut-block. The bioenergy market (and especially the pellet market) is expected to continue to grow rapidly, in particular in Europe (Sikkema, 2011). In the United States, a recent study (US Department of Energy, 2011) showed the linear dependence of the expected rise in the market and the price for feedstock derived from forest harvesting residue. By 2030, given only proven technology, at $20/dry ton about 10 million dry tons/year would be taken. But at $80/ton the expected harvest would be 45 million tons.

The two main impediments thus far to increased slash usage for biofuel has been the construction of adequate mill capacity, and the cost of transporting slash to the mill. For example, transportation on a spur road costs $7/green ton vs $0.18 on a highway (US dollars; Pan et al., 2008). Thus, slash has tended to be used as a feedstock only when the harvest block is near a highway. However, transportation costs can potentially be greatly reduced by on-going research efforts to decrease the bulk density of slash by converting it to biofuel *on-site* with mobile biomass conversion technologies (Li et al., 2015; Han et al. 2004). These new methods produce products such as biochar, torrified pellets, and dense briquettes, and are projected to reduce transportation costs dramatically on gravel roads by insuring that trucks are carrying compact small pieces of converted wood with low moisture content. Thus, the future is one where slash in any harvested site is an economically attractive feedstock. If this emerging technology proves viable, then the projections for slash consumption mentioned above will need to be drastically increased, as they were based on existing technology.

While the proportion of cut-blocks undergoing woody residue extraction is expected to rise steadily in industrial nations with considerable forest cover (Swedish Forest Agency 2013; Gan and Smith 2006), slash removal can potentially have negative consequences. First, the removal of the woody residue may adversely impact the growth of the subsequent forest (naturally recruited or planted) in areas such as North America where fertilizers are less frequently employed (cf. British Columbia vs Sweden: Swedish Forest Agency 2013; British Columbia Ministry of Forests 2013.) Second, slash represents crucial habitat for many taxa, and thus its loss might reduce the abundance of some species, or, in the worst case, drive them to local extinction. As Dalhberg et al. (2011) point out, it is especially useful to focus on the effect of the loss of fine woody debris as this is the predominant component of slash.

Concurrently, many have noted the beneficial effects of slash retention on soil, tree growth and to some degree, biodiversity. While many studies have considered the effects of varying total quantities of retained slash, very few studies of soil fertility, growth or flowering have differentiated between slash left as discrete piles and windrows vs residue more uniformly distributed over the cut-block. The default assumption, typically implicit, is one of spatial dispersion.

On nutrient-poor sites, whole-tree harvesting, although relatively inefficient (Briedis et al., 2011), leads to reduced soil nutrient status (Jacobson et al., 2000). A decrease in available nitrogen and other nutrients due to slash removal has been reported in several studies (all short-term); where found, these decreases tended to slow tree growth for at least the first 10-20 years of a rotation (Jacobson et al., 2000; Egnell, 2011, Thiffault et al., 2011).

Several studies have shown that logging residues are beneficial for understory plants (e.g. Olsson and Staaf, 1995; Åström et al., 2005) for reasons having nothing to do with fertility. It is presumed that the ameliorative effect is due to reduction in near-surface wind speed and diurnal soil temperature fluctuation, thus increasing water retention (Mahendrappa and Kingston, 1994). The enhanced water availability also promotes sexual regeneration during the establishment stage (Smith, 1951; Alexander, 1987; Greene et al., 1999). Likewise, establishment of many bryophyte species is poor when slash is removed (Bråkenhielm and Liu, 1998; Busby et al., 1978).

Importantly, and not surprisingly, many studies report that maintaining woody residue in post-harvested sites with a range of age, size, state of decay and from a number of different tree species is beneficial to wood decay and other fungi (e.g. Heilmann-Clausen and Christensen 2003; Bunnell and Houde 2010), as well as to many species of invertebrates. Fine woody debris is mainly composed of small branches and twigs whereas coarse woody debris can be divided further into standing dead wood and downed logs/branches. The physical characteristics of dead wood vary with time and depend on several factors including size, temperature, moisture and position (standing or downed) (Harmon et al., 1986).

Many beetle species are dependent on fine and coarse dead wood, in a variety of both size and decay classes. A number of studies have shown that beetle diversity is lowered where slash has been removed from a harvest block (e.g. Gunnarsson et al., 2004).

Several studies have argued for the importance of downed woody debris for small mammals. In some cases it represents a refuge from predators (e.g. cotton mice, *Peromyscus gossypinus*: McCay, 2000). In other cases, it provides food for predators (e.g. invertebrates for the red-backed vole: Ucitel et al., 2003). Lower capture rates and densities of small mammals have often been found in sites where woody debris had been removed (e.g. deer mice: Lee, 2004; shrews: McCay and Komoroski, 2004; Cromer et al., 2007).

In short, there are arguments for removal of slash removal (biofuel; fire hazard) and for its retention (benefits for plants, fungi, and many animals). The majority of the relevant literature focuses on the quantity of slash that is, or should be, retained on any given cutblock; a small minority focuses on the distribution of FWD within a metapopulation. However, in addition to the importance of FWD availability over time within a landscape, what is important for maintenance and promotion of ecosystem services and biodiversity i*s not only the total amount of slash retained but its spatial aggregation*. Despite this, there is not a single study that investigated the effect of aggregated slash on the abundance and presence of flowering plants or on soil fertility prior to McCavour et al. (2014), and only a handful of studies even mention spatial array; once again the default assumption in the literature is that of spatial dispersion.

Given that soil nutrients may vary markedly at the scale of a meter (Jackson and Caldwell, 1993) and, as shown by McCavour et al. (2014), effects of piles on soil fertility may extend only a few meters from the edge, spatially explicit studies of the effect of FWD on soil nutrient availability are needed. Studies that compare only different blocks, with or without slash, or that compare blocks with slash remaining as piles vs. those where slash is distributed uniformly, will be problematic because the spatial distribution should have quite different effects on the soil nutrient status, plant yield and diversity.

The spatial pattern of post-harvest residue becomes especially important when considering its effects on species competing with the planted crop. One expects uniformly distributed slash on coarse soils to enhance nutrient availability more evenly, and for a shorter period of time, than would piles or windrows because a much larger percentage of the wood is in contact with the ground. For example, Morris (2009) found increased concentrations of dissolved organic N (DON), soluble organic N (SON), and soil organic N following distribution of chipped wood across a harvested plantation area than without the chipped wood. However, an even distribution will not delay canopy closure anywhere within the harvest block as the crop grows. By contrast, piles and windrows will release nutrients relatively slowly and enhance available light (by locally delaying canopy closure of the species planted among the aggregations of residue).

The local magnitude and distribution of slash is also important. Clearly, an evenly-distributed loading of 0.2 kg/m^2 is insufficient to provide shelter for a deer mouse because the FWD loading would be discontinuous. Depending on when and how cutblocks are harvested, habitat availability within the metapopulation may be patchy (to the point of dispersal limitation), with times of zero availability as dispersed slash decomposes relatively fast, to 75% loss within 25 years (Tarasov and Birdsey, 2001). Conversely, as the top of a large slash pile (say >30 kg/m^2) decomposes, it will maintain habitat for fungi and invertebrates relatively longer, and offer an open space and high nutrient availability for intolerant early successional flowering plants long after canopy closure has ensued in the adjacent plantation. Spatial realism requires including the ability of organisms to move. For beetles this would involve primarily the movement of sexually mature adults whereas for lichens and fungi it would entail the dispersal of spores. Unfortunately, there is almost complete lack of knowledge; dispersal ecology being in its infancy for these taxa and not substantially more developed for plants.

The concept of metapopulations, first introduced by Richard Levins (1969), was slowly developed to the point where it was useful for field-oriented field studies (Hanski and Gilpin 1997). This literature has produced two main conclusions. The first is that populations are typically ephemeral because the habitat patches they occupy are also ephemeral. For example, an old growth specialist will lose its patch when an intense, stand-replacing disturbance takes place. A more pertinent example would be a beetle species that uses the larger-diameter fraction of FWD in shaded conditions as a primary habitat for its larvae. Given the stochasticity of FWD deposits to a forest floor in a managed landscape, FWD habitat patches would be found in an industrial forest landscape in pulses. The point of the theory is that any one population may become extinct (local extirpation), or fall to unsustainably small numbers, but the *meta*population persists because dispersants from existing populations can colonize new habitats as they arise. The long-term persistence of the metapopulation depends therefore on (1) the rate of extinction within patches, (2) the rate at which new patches arise, and the (3) rate of dispersal among patches. Those rates can also fluctuate on varying time scales, for example, from the time scale of a harvest cycle, to that of a single event such as an ice storm to that of climate change. Contributing to the knowledge gap and hence ability to recommend appropriate forest operations is the assumption by some models, such as in Dahlberg et al. (2011) that (1) and (2) are equal; therefore species diversity is largely dependent upon dispersal rates.

Given how little we understand the population ecology of the hundreds of species utilizing slash or FWD, modelling population dynamics with slash quantity and distribution may seem difficult; but one could develop a metapopulation simulation for the fungi and lichen species using existing knowledge of spore dispersal and population growth rates until such time that we have collected the relevant life history data for each of the species under consideration, especially the rate of increase in abundance under specific habitat conditions.

The second main point of metapopulation theory is that the metapopulation will persist for some interval even after the number of available habitat patches has fallen so critically low that extinction has become inevitable. This is referred to as "extinction debt" (Hanski and Oveskeinen 2002).

Given that little is known about the vagility of most invertebrates, and many fungi, one might consider erring on the side of precaution when planning how much slash, or many slash "patches" to harvest, so as to avoid creating an extinction debt before adequate data is collected and analyzed. Further, as we will see in Chapters 3, very small and very large quantities of slash lead, for different reasons, to extremely low establishment rates for plants.

I turn now to a review of the effects of slash removal by whole tree harvesting on three taxa: plants, fungi, and saproxylic invertebrates.

Plants

The great majority of what we know about the effect of slash removal on plants is concerned with commercially-valuable trees. There is remarkably little literature concerning the effect of WTH on shrubs and herbaceous plants, and even less on the growth rates of plants or their age-specific survivorship as affected by WTH; the great bulk of the literature concerns effects on soil nutrient availability. I begin below with a review of nutrient loss as a consequence of WTH and then turn to what is known about the effect of WTH on trees and, in more detail, shrubs and herbaceous plants.

Nutrient availability and whole tree harvesting

About half of the nitrogen in a tree is in the top of the stem and the branches (Nisbet, 1997; Cramer, 1974). As summarized by Thiffault et al. (2011), most studies (e.g. Little and Klock, 1985; Ponder et al., 2012) found no significant adverse effect of WTH on concentrations of soil nitrogen or carbon in the first decade or two, although there are exceptions (e.g. Mann et al., 1988). Phosphorus and calcium are more consistently negatively affected (Thiffault et al., 2011). The loss of potassium is somewhat lower but still substantial (e.g. Boyle and Ek, 1973). Where WTH-related nutrient differences are detected, they appear to be more serious in the organic layer than in the underlying mineral soil, and are discernable about one decade after harvesting (Thiffault et al., 2011).

There is perhaps an emerging consensus that the initial lack of agreement among studies is due to site differences: stands on coarse soils, with their low soil nutrient status, are among the most likely to be negatively affected by WTH. For example, Morris et al. (2014) could only find an effect of WTH in black spruce stands on sandy sites. Likewise, Himes et al. (2014) argued that only nutrient poor sites were at risk from intensive slash removal.

Given the paucity of empirical studies on WTH effects over time periods of more than two decades, longer-term appraisals can only be obtained from modeling. Abner et al. (1978) modeled changes in forest floor organic nitrogen availability following slash removal and found that it declined for the first 15-30 years and required 60-80 years to recover to pre-cut levels. Himes et al. (2014) argued that long-term nutrient depletion would only happen with intensive residue removal on soils low in available nutrients. Thiffault et al. (2014b) likewise identified pre-harvest nutrient status as an important indicator in assessing long-term risk.

Because of the lack of very long-term studies, most jurisdictions have placed a limit on the amount of woody residue that must be retained (generally 20-30%). The review of Thiffault et al. (2014a) showed that present forest operations are not particularly efficient and that we are seldom near the limit set by law: typically world-wide only about 50% of residue is removed by WTH (the maximum value in their meta-analysis was 89%). The concern among some scientists and informed citizens is that residue removal efficiency will improve dramatically if the biofuel industry resolves the economic problems discussed above.

The question arises: does this tendency toward a loss in soil fertility on poor soils affect the yield of commercially valuable species and non-arboreal plant diversity? In what follows, I review some broad WTH and slash effects, not focusing solely on soil nutrients.

Trees

Many studies have looked at the effect of slash or its absence on the natural recruitment of tree species or on planted stock (e.g. Mann, 1984; Egnell and Valinger, 2003; Waters et al., 2004). This work has typically been done with paired plots.

For asexual reproduction, Mann (1984) found that WTH in hardwood stands reduced basal sprouts for all species, relative to tree-length harvesting. The author speculated that the result was due to stump damage during the WTH operation. Certainly, the shade provided by slash could have little beneficial effect on the rapidly-growing basal sprouts: the stems would typically be taller than the slash within a year or two, and the well-established root system means that transpiration is not a major factor in initial post-harvest survivorship as the initial root-shoot ratio will be huge.

Turning to sexual reproduction, there appears to be a contrasting effect of WTH on natural recruitment density vs mean growth rate. Mann (1984) showed that most of the hardwood species established more seedlings if residue was removed. He attributed this result to greater disturbance of the Of layer as trees were dragged across the harvest block. Scherer et. al. (2000) found that the same accidental scarification of the Of by WTH also increased the abundance of ruderal ("weedy") species. Given the small size of plant seeds at higher latitudes, the germinants are necessarily small (typically one to a few cm for the hypocotyl length (Hesketh et al., 2009). Thus, an intact Of layer in an open, dry clearcut represents a poor substrate for any species with a seed smaller than *Acer saccharum* (40 mg; Greene and Johnson, 1998). On the other hand, slash can offer shade and thus soil moisture retention while root systems are still small (Olsson and Staaf, 1995; Bråkenhielm and Liu, 1998; Åström et al., 2005). In consequence, one might expect that a WTH operation will increase the initial density and survivorship of natural regeneration by exposing better microsites for germination and establishment, but will reduce subsequent survivorship for the critical first two years (Greene et al., 1999). On the other hand, on a coarse soil, the higher surface temperature following WTH may well reduce the establishment success significantly.

Given these many ways in which soil texture and WTH can interact, it is not perhaps surprising that a meta-analysis may indeed reveal a great deal of noise among studies (Thiffault et al., 2011), depending on what was measured (growth or survivorship) and for how long. This lack of agreement can be attributed not only to these contrasting effects of WTH, but also to confounding factors such as dispersal constraints and the quality of the seed years occurring just after harvest (Greene et al., 1999). A methodological caveat involves studies where an investigator experimentally removed woody debris but did not modify the Of layer. The result of such an experiment will be a poor guide to what WTH engenders *operationally* because we have separated the accidental scarification from the shading effect.

We expect that height growth should be better for the small germinants typical of the boreal/hardwood transition forests because of the shading provided by the FHR, at least until the seedlings have grown taller than the residue. Indeed, many studies have shown that artificial shading greatly improves both height growth and juvenile survivorship, especially on intrinsically droughty sites (e.g. fluvioglacial sands; southern aspects in dissected terrain in North America) or in dry summers (e.g. Mann, 1984; Greene et al., 1999; Egner and Valinger, 2003). Further, the residue can act as a mulch, reducing water loss from the exposed mineral soil that typifies the more clement microsites for small germinants. Conversely, if most of the natural recruits on a site with residue present are growing on thick organic layers, then their height growth will be initially poor. These varying effects may partially explain the contradictory results in the literature on early growth rates with and without FHR (Thiffault et al., 2014a). That is, during the first decade after harvesting, the positive shading and mulching effect on non-WTH sites may be balanced by the poorer growth that occurs until root systems have reached the mineral soil under the Of layer.

There is a large literature on the important role played by the fraction of rotted CWD with the larger diameters in the recruitment dynamics of shade tolerant but small-seeded (e.g. in North America, *Tsuga* spp. or *Betula alleghansiensis*) species in intact northern forests. Given the almost complete absence of exposed mineral soil in an undisturbed forest, large decomposed logs or woody pieces are the only suitable substrate as their height allows the wind to re-entrain falling leaves, and thus these downed logs present no mechanical obstruction for small germinants (Greene et al., 1999; LePage et al., 2000; Simard et al., 2003). WTH will remove far more of these suitable pieces than would cut-to-length harvesting.

Further, contrasting harvesting styles during the previous century have had discernable effects on tree regeneration. Weaver et al. (2009) showed that small-seeded tolerant tree species (e.g. *Picea rubens, Tsuga canadensis, Betula alleghaniensis*) had much lower recruit densities in >50 year-old forests that had been clearcut than similar-aged forests that had been selection-cut. The recruitment of larger-seeded tolerants such as *Abies balsamea* and *Acer rubrum* were far less affected by the cutting history. Weaver et al. (2009) attributed these differences almost entirely to the paucity of rotted CWD in the former clearcut.

Above, I focused on larger CWD not merely because of leaf re-entrainment but also because diameter affects decay rate. It is assumed that the great majority of decomposition is due to fungal metabolism and this accounts for about 70% of the total loss (Chambers et al. 2000). Large diameter pieces have a low surface-to-volume from which water will evaporate slowly after rain. In the xylem, this retention can impede oxygen diffusion and thus slow fungal metabolism (Harmon et al. 1986). At the other extreme, very small pieces of FWD can lose water so quickly that this also limits fungal growth (Tuomi et al., 2011). Indeed Tuomi et al. (2011) argue that the smallest of the FWD (1 cm twig tips) may actually decompose somewhat more slowly than FWD in the 5-10 cm range, and there is some empirical support for this for *P. sylvestris* (Vavrova et al. 2008).

Using the empirical results of Tarasov and Birdsey (2000) for Norway spruce, a small-diameter residue class (midpoint of 12.5 cm) should have 35% mass loss after one decade, whereas wood pieces in the 50 cm (midpoint) class would have lost only 10%. Palvainen et al. (2004) reports that small Norway spruce branches <10 cm diameter had 20% mass loss after 10 years. Turning our attention to greater ages, Tarasov and Birdsey's (2000) empirical work showed that by year 25 the 12.5 cm diameter class had a 75% mass loss, while the larger classes had lost about 50%. We can assume that for the 5-10 cm class (i.e. the larger of the FWD), decomposition (defined as 10% mass remaining) would be complete by year 25, given that pieces about twice as large have lost 75% of the mass by that date and complete decomposition is defined (Dahlberg et al. 2011) as 90% loss. In summary, the nutrient pulse from the FWD and smaller CWD occurs early in the rotation but is nonetheless several decades in duration. We should not be surprised if understory plants, which tend to reproduce sexually only when light levels suddenly increase (e.g. a natural canopy gap or a harvest), show a negative response to WTH.

Understory plants

While interest in the biodiversity of understory plants in areas where commercial forestry is practiced is recent, nonetheless some generalizations can be made. First, understory plant communities in stands with a strong hardwood component tend to be much more diverse than stands dominated by conifers (Macdonald and Fenniak, 2007; Hart and Chen 2008.) Second, the density of the understory layer of herbs and shrubs is important as it affects the regeneration of trees (Roberts, 2004; Royo and Carson, 2006). Third, with increasing time since disturbance there are increases in the proportion of plants that are shade-tolerant or possess vertebrate-dispersed fruits (Aubin et al., 2009). Finally, there is competition for light and nutrients both between shrub and herbaceous layers as well as among the species within these strata (Chavez and Macdonald, 2010).

The effect of slash removal

Despite increasing concerns about the impact of WTH on the species composition of the non-arboreal components of forests (Dynesisus et al., 2008; Fridman and Walheim, 2000), research conducted to date on understory vegetation has been restricted to a few abundant plant species on small experimental plots (e.g. Bråkenhielm and Liu 1998; Bergquist et al., 1999). Indeed, I have found only one study (Åström et al., 2005) that assessed the impacts of *commercial level* slash harvesting on understory bryophytes or vascular plants. Experimental removal of slash can imitate certain aspects of WTH but not the accidental scarification due to skidding logs.

Several studies have shown that logging residues are beneficial for understory plants (Olsson and Staaf, 1995; Bråkenhielm and Liu, 1998; Åström et al., 2005). In clearcuts, slash reduced near-surface wind speed and diurnal soil temperature fluctuation, and thus increased water retention (Mahendrappa and Kingston, 1994). In consequence, the more desiccation-sensitive species (typically late-successional), and many bryophytes, do poorly when slash is removed (Bråkenhielm and Liu, 1998; Busby et al., 1978). More shade-intolerant species can increase in abundance following slash removal (Åström et al., 2005) but this is less common. At the stand scale, conclusions about the effect of WTH on diversity are as equivocal as with conventional logging. Slash removal has been reported to cause both increases and decreases in species diversity (Kardell, 1992; Åström et al., 2005; Bergquist et al., 1999). Bergquist et al. (1999) found relatively small effects of slash-removal on biodiversity except for dwarf shrubs in the oldest post-harvest stands, but only three species accounted for about 95% of this shrub biomass.

Astrom et al. (2005) provide the only wide-ranging study of slash removal effects on plants using commercial operations rather than small scale experiments (although the stands were only 5-10 years post-harvest). They found that bryophyte diversity decreased markedly following slash removal; the microscale shading provided by slash may therefore be crucial for bryophyte persistence until herbaceous cover can re-establish and provide shade. Bryophytic species typical of open areas were unaffected by slash removal as was the diversity of vascular plants; the authors could find only 4 of 131 plant species whose abundance had been significantly affected by slash removal, and three of these showed an increase. Given that the vast majority of the leaf area of regenerating herbs will be from asexual regeneration, and given that a relatively small portion of a harvest block is physically affected by the dragging of trees in a WTH regime, this lack of response to WTH by the pre-harvest species is not surprising.

The same arguments about the effects of WTH-induced soil nutrient depletion leading to poorer growth of trees on coarse soils could also be applied to understory plants. In particular, it ought to lead to differential success depending upon the tolerance of species to limitation of particular nutrients, and thus should lead to changes in species composition. Unfortunately, there are not yet any long term permanent plot studies of understory species' responses to the changing nutrient status created by WTH. As with trees, it is only in the second decade that any nutrient-induced effects on growth or survivorship become apparent; available studies with herbs and shrubs do not extend past a few years. Reduced soil pH, a typical consequence of slash removal (Thiffault et al., 2011), can negatively affect plant species, especially bryophytes whose establishment is typically stimulated by high pH (Olsson and Kellner, 2002; Egnell et al., 1998). Slash harvesting can negatively affect vascular plants in other ways: e.g. by reducing nitrogen inputs (Olsson and Staaf 1995; Bråkenhielm and Liu 1998). Nonetheless, it seems unlikely that these edaphic effects greatly affect biodiversity in a WTH regime in the short term, given the primacy of asexual recruitment for herbs and shrubs.

As with clearcutting generally, slash removal further benefits the more shade-intolerant early successional species. Scherer et al. (2000) examined a number of understory plant responses to various slash treatments (chopped, piled and burned, burned, and untouched), and found that slash treatments caused an increase in abundance of weedy species that were not normally present in their mixed eastern Washington forests. This may well be due simply to the uncovering (lack of FHR) of substrate, and thus there is merely more space where ruderal seeds can germinate. It is also possible that ruderals, typically less nutrient-demanding than more competitive plant species, thrive in an area lacking the initial first flush of nutrients from the FWD. That is, their more-demanding competitors may simply be growing more slowly than "normal" and thus competitive exclusion rates are slowed (Tilman et al., 1999).

It is well-known that many moss species, like trees, rely on well-rotted CWD as a spore germination substrate (e.g. Rambo and Muir, 1998). However, there has been much less interest in the rooting media of understory plants. Recently, and not surprisingly given what we know from the extensive research on tree species in relation to seed size, Six and Halpern (2008) showed that the smaller-seeded understory plant species tend to be found preferentially on well-rotted CWD; these comprised about 20% of the species they studied in coniferous stands in the mountains of Washington. Indeed, Lee and Sturgis (2001) found distinct herbaceous communities on CWD vs the Of layer in a 30-year old aspen forest.

The fact that paper birch and aspen can be reliably regenerated asexually without herbicides means that understory plant persistence in situ may be quite different for planted conifer stands vs these naturally regenerated hardwood stands. Application of herbicides in conifer plantations does not necessarily have a long-term pernicious effect on understory species because the chemical removal of the fast-growing hardwoods means that the light environment is far better for the understory plants for the first decade than it otherwise would have been (Man et al., 2009; Man et al., 2010). Knowing nothing else, we would expect that the understory species typical of hardwood stands should therefore show a more dense cover as well as a tendency for fewer ruderals. However, I can find no direct comparisons of post-harvest understory plant response in hardwood vs conifer stands where the application of herbicides is explicitly examined.

Landscape-scale persistence of understory species under a regime of intense harvesting is not understood. Duffy and Meier (1992) presented a long chronosequence from clearcut Appalachian forests indicating that even a century is not sufficient time for species richness and cover to reach the levels found in intact forest. This would make sense if (1) some species are especially harmed by clearcutting and (2) seed dispersal for most species is sharply constrained.

Unfortunately, Duffy and Meier (1992) do not report which species or functional groups appear to be missing from their lists from primary forests. Further, as argued by Cain et al. (1998) our understanding of dispersal beyond a few meters for understory herbs and shrubs is quite rudimentary. Most species appear to have primary seed movement of perhaps 1 meter or less via ant dispersal or explosive dehiscence. Subsequent dispersal is perhaps quite extensive, due to the movement of seeds through the intestinal tracts of ungulates such as deer as well as omnivores like bears, but this remains poorly understood (Myers et al., 2004).

In short, we do not know if the species diversity of forest herbs and shrubs will be dramatically affected at the landscape scale in the long term by WTH. The only study we could find approaching a century is that of Duffy and Meier (1992) who used the problematic approach of a chronosequence, and they did not examine WTH effects. Conversely, an array of uncut, old growth corridors that might be used by ungulates carrying ingested seeds could greatly ameliorate the effect of increasing harvest intensity on the hardwoods (Lindenmayer et al., 2000).

In conclusion, one can make the informed speculation that more intense harvesting of higher latitude forests coupled with more intense removal of FWD and CWD will have the following effects. First, the abundances of ruderals will increase while more tolerant late-successional species will become less common. This increase of ruderals will only apply to the first post-harvest decade in a hardwood block as the rapid growth of trees will quickly shade out the more light demanding ruderals. Second, small-seeded tolerant tree species may be reduced in abundance as there will be, after the next rotation, essentially no available stands with CWD sizes adequate for sexual recruitment. Thus, the persistence of these species will depend evermore completely on asexual reproduction following each harvest. Finally, those tolerant understory species with the most restricted dispersal at the scale of a kilometer will tend toward ever greater declines in abundance.

Nonetheless, one speculates that there is no reason to expect landscape or regional-scale extinctions of any understory species unless there are small-seeded, tolerant species with dramatically limited dispersal capacity. Since nothing is known about seed dispersal at this spatial scale, one cannot say whether such worrisome species exist or not.

Fungi

There are few studies on the effects of different harvesting methods and slash on fungal biodiversity. Most of the relevant literature investigates clearcut harvesting (with minimal discussion on slash removal and other specifics about the methods) and its effects on a few of the fungal groups, such as mycorrhizae and wood decay fungi. Part of the problem with studying fungi is general lack of knowledge of their diversity and autoecology (Lonsdale et al., 2008). Much of what can be concluded derives from piecing together evidence from studies on the effects of fungi from clearcuts vs uncut forest, and the general effects of harvesting on within-block site conditions.

While the literature discusses the effects of whole tree vs. tree-length on plant diversity, tree growth rates, productivity and soil conditions (see the previous section), the effect of these different practices on fungal diversity has been much less widely researched except perhaps in Scandinavia.

Whole tree harvesting and fungi.

Studies on dead wood management show that retaining logs and slash of different age, size and state of decay is important to the maintenance of wood decay fungal diversity (Heilmann-Clausen and Christensen, 2003; Bunnell and Houde, 2010). In mixed stands, wood decay fungal diversity was proportional to tree diversity (Rajala et al., 2010), suggesting that for mixed species dead wood diversity is an important contributor to fungal diversity. That is, only leaving behind a few commercially unimportant tree species (e.g. *Betula papyrifera* in the boreal) as slash or standing trees may not be as beneficial for the fungal community as a whole as would leaving a wider variety of tree species.

Coarse woody debris typically has a succession of fungal species during the decay process (Bergland et al., 2005; Küffer and Senn-Irlet, 2005) and species diversity may be influenced by wood density and quality. In a study in Scandinavian boreal forests, fungi engendered faster decay rates in trees that grew fast, and slower decay rates in trees that grew more slowly. This may indicate a shorter time period for wood decay fungi to colonize the living tree in managed forests when compared to old growth forests, which could negatively affect those fungal species with poorer dispersal abilities (Edman et al., 2006). The same study detected variation in the decay capacities of the saprophyte of *Phlebia centrifuga.* This points to the possible role that genotypic variation within species may play in fungal successions as well as species assemblages.

Some studies indicate that fungi on logs in clearcuts have higher diversity than those in the forest, especially the polypores (Junninen et al., 2007; Küffer and Senn-Irlet, 2005), and that they can tolerate high light conditions if the quality of the wood is appropriate. Overall, for CWD a range of species, age, size and quality is required to maximize fungal diversity. Harvesting practices that ensure any of these site factors would be more likely to maintain wood decay fungal diversity after harvesting. Whether this is a sufficient amount of CWD, and varying enough in size and quality for wood decay fungi to thrive in the long-term -even without an increase in slash removal intensity- is not known.

Fine woody debris (FWD) from slash is also an important habitat for wood decay fungi and is often a refuge for many species in disturbed forests (Küffer and Senn-Irlet, 2005). Fungal species richness in slash was found to be only about half as great in clearcuts from younger forests as in slash from old forests, and an even more pronounced difference in richness was found between slash and naturally occurring FWD in old growth forest (Allmér, 2005). By contrast, Allmér et al. (2009) found that removing logging residues from coniferous stands had no effect after 25 years on litter layer saprotrophic fungal richness or frequency of abundance, pointing out that apparent short-term effect may be negligible in the long term. The authors stress that the study involved only abundant species and that no conclusions could be drawn about rare species.

Effects at larger spatial and temporal scales may be important (Allmér et al. 2009). If for example a number of adjacent stands were harvested at the same time, a short-term decline in FWD decay fungi may have long-term effects due to dispersal constraints. However, because FWD occurs more readily in managed forests, and fungi occurring on FWD are less specialized and not subject to long successions, inputs of CWD in managed stands may be of greater importance.

As is the case with wood decay fungi, there is a large body of research on the effects of logging on ectomycorrhizae (EM), although the specific effects of whole-tree vs. other methods have not been investigated. Studies most often involve clearcuts and the details of harvesting practices rarely indicate if and where slash was deposited or removed. In general, EM communities have shown (1) an increase in negative affects with increasing harvest intensity (Lazaruk et al., 2005; Kranabetter and Wylie, 1998); (2) a significant difference between harvested and unharvested, or regenerating forest (Summerbell, 2005; Jones et al., 2003); and (3) a negative effect of larger gap sizes and distance from forest edges (Durall et al. 1999; Hagerman et al. 1999a). Quick regeneration of hosts and limited soil disturbance were suggested as the reason why occasionally EM communities show no effect of logging (DeBellis et al. 2006). Harvesting practices that minimize soil disturbance from machinery and dragging of logs (WTH), and encourage plant regeneration by limiting the size of cuts and using green tree retention patches, would best serve the EM fungal community reestablishment in post-harvest sites.

The ability of some fungi to essentially switch functional groups may be an important adaptation in disturbance-prone systems such as the boreal forest. An abundant EM fungal genus *Piloderma* has been associated with the presence of woody debris (Smith et al. 2000) and may live as saprophytes when conditions require them to do so (Erland et al., 1990; Hagerman et al., 1999b). There is evidence that some EM fungi can take up organic N by using proteolytic enzymes (Cairney and Burke, 1994; Dahlberg, 1997; Cairney and Burke, 1998). This indicates that woody and litter layer debris in clearcuts may be important for the continuity of some EM species as reservoirs for live mycelium and for colonization by fungal spores. Once seedlings were present, fungi could switch to mutualisms, supplying vital nutrients and minerals to establishing plants.

In general, harvesting has a greater effect on EM composition than on diversity; that is, species that colonize roots after harvesting tend to be different than those that colonize roots in the forest (Jones et al., 2003; Heinonalo et al., 2007). It is presumed that this compositional change is a result of changes in the physical and chemical properties of the soil, and the loss of inoculum. Short-wood harvesting is considered to have less of an environmental impact than other conventional harvesting methods, because it is amenable to partial and selective cutting, the use of skidders is rare, and slash is left on-site. It is therefore probable that this method would be less damaging to soils and more beneficial to EM community retention and recolonization.

Soil compaction has also been shown to affect nutrient levels and microbial communities (Côté et al., 2000; Ballard, 2000; Palvianinen et al., 2005). Harvesting techniques that result in the least soil compaction, by reduced use of larger machinery, or the limiting of the machinery to a small portion of the cutblock, would be most beneficial to fungal communities. WTH in most cases involves dragging trees, which causes soil disruption and compaction. Heavy slash was found to reduce soil compaction in CTL (cut-to-length) sites (Han et al., 2009). This suggests that CTL combined with heavy slash retention would cause the least damage to physical soil properties and therefore be more beneficial to soil and EM fungi (Lonsdale et al., 2009). Soil fungi have been shown to recover quickly and to pre-harvest levels in clearcuts when compaction is minimized (Housten et al., 1998).

Different types of mycorrhizae form on fine root tips at characteristic soil depths. On *Populus tremuloides* root tips in a three-year-old clearcut, arbuscular mycorrhizae (AM) preferred mineral soil at lower depths, while EM preferred shallower organic soils (Neville et al., 2002). Soil disturbance of organic layers is common in clearcuts (Marshall, 2000) and any harvesting method that disturbs soils (e.g. by skidding logs) may cause larger loss of EM than AM, but both could be susceptible when soil disturbance is severe or organic layers are shallow.

Foliar endophyte communities would most likely be affected by all the methods of harvesting that result in complete tree mortality in the cut. Some foliar endophytes have the ability to behave as saprotrophic fungi (Stephani and Bérubé, 2006) and these species might benefit from slash remaining in the cuts. Species that are obligate on the foliage would be affected to a greater extent by the removal of host trees and may take longer to recover after clearcuts. Clearly, retention would aid in their persistence. The species composition of needle endophytes on different pine species has been shown to change with needle age, indicating that seasonal events such as needle emergence and maturation will affect the fungal endophytic community composition (Hatam et al., 1998). This may mean that foliar endophytes would be more susceptible to harvesting undertaken during certain seasons.

In fragmented landscapes, dispersal is the key factor when considering fungal biodiversity at a landscape scale, with available habitat, habitat colonization, and microhabitat associations all being important factors for fungal dispersal (Jonssell, 2007). An unknown degree of green tree retention and slash retention are presumed to be required for the maintenance of fungal biodiversity (Penttilä et al., 2004). If we knew the probability distributions for spore dispersal and colonization success for even a few "representative" species from each functional group, we could attempt to model the landscape scale dynamics and thus arrive at recommendations for foresters. As it is, one pictures merely "tweaking" present practices and hoping for the best. Others such as Hartmann et al. (2010) believe a switch from Integrated Forest Management practices to high yield plantations and forest zoning (a variant on the Triad concept) would better protect biodiversity at larger geographic scales.

Studies that examine the time periods of various life stages (such a fruiting body life span) and at what scale specific fungal communities have reached an equilibrium in species composition would greatly aid in our understanding of how fungi may be affected by different harvesting methods and rotations at stand and landscape levels. Bergland et al. (2005) showed that polypore populations are stable at the stand level and surveying at this scale would give a good indication of the effect of harvesting on this fungal group.

The best predictor of fungal species richness in old growth forest islands in Scandanavia was area, with stand structure being the second highest predictor, and isolation the lowest. Area predicted variation in richness best for red-listed fungi and substrate specific fungi, whereas stand structure variables explained richness in different groups suggesting species richness of one group is not a good overall indicator (Berglund and Jonsson, 2001). Rotation intervals around the world are almost invariably <100 years. Yet some ectomycorrhizae are clearly associated with old growth forest (Visser, 1995; Dahlberg et al., 1997; Bradbury et al., 1998). In the short term this would mean reduced occurrence of these fungi, and, in the long-term, possibly regional extinctions. As wood decay fungi rely on a range of logs differing in size and species' identity, and in close proximity to other CWD-rich sites (Edman et al., 2004), it would be logical to argue that the elimination of older stands would have a detrimental effect upon wood decay fungal diversity at the stand and landscape levels. Again, the tendency of WTH to remove the smaller CWD in the slash will exacerbate the problem.

In Sweden, as little as 5% of the forest is old growth and this remnant is highly fragmented (Bernes, 1994). In Finland 40% of threatened fungal species are assumed to be dependent on old-growth forest (Penttilä et al., 2004). In Sweden 25% of threatened species are thought to occur largely on old growth trees or logs (Berg et al., 1994). The consequences of this are complicated by the fact that so little is understood about the biodiversity of fungi in forest ecosystems or even, for many species, their basic autoecology. The ignorance is largely due to a lack of interest by scientists: Lonsdale et al. (2004) point out that in a random sample of 100 papers dealing with species-richness of different taxa, fungi were among the lowest at 2%.

In the worst case scenario where all woody debris (slash and any stumps or larger woody branches) has been removed, and there are neither snags nor residual live trees, this would effectively mean the absence of FWD for long periods and of CWD forever. In this scenario no wood decay fungi could exist as no habitat would be available for them. Some species may be present in the soil as spores or possibly mycelium from within the stand, which in the very short term could act as sources of inoculum. The length of time resistant propagules and mycelia would be viable would depend on the species and other site conditions (dryness, exposure, erosion). Spores from other stands (dispersal capabilities allowing) could act as sources of inoculum for the future for the FWD.

Invertebrates

While many invertebrates such as slugs or spiders may be affected adversely or positively by the loss of residue and thus of shading, ease of predation, or protection from predators, I focus here primarily on the most susceptible organisms, the saproxylic invertebrates, defined as those dependent, during some part of their life cycle, upon the wood of dead or dying trees and shrubs (Speight, 1989). Despite their common dependence on dead wood, saproxylic invertebrates exploit this resource in different ways and distinct communities can be associated with dead wood of a certain size, position, tree species and degree of decomposition (Grove, 2002; Jonsell, 2008a; Simandl, 1993; Ulyshen and Hanula, 2010). In turn, this variety of exploited niches means that forest harvest residue (FHR) removal will have differing effects on members of this guild. After a brief review of the autoecology of invertebrates feeding on snags or FHR, I will turn to the effects of harvesting on these taxa, and its consequences for landscape scale species persistence as well as intraspecific genetic diversity.

With respect to the needs of invertebrates, forest harvest residue can be separated into coarse and fine woody debris (CWD and FWD, respectively) according to its diameter class; the size limit between coarse and fine varies between studies, ranging from 2.5 cm to 15 cm depending on forest type and research goals (Harmon et al., 1986).

Hammond et al. (2001) evaluated the effect of position (or type) of coarse woody material on the species richness and abundance of saproxylic Coleoptera. They cut live aspen trees, leaving a high stump (120 cm) and cut two more sections, one left on the ground as a downed log and another suspended 1-2 m off the ground to mimic a snag. They found that snags contained greater numbers of beetles than high stumps or logs, although species diversity did not differ. Interestingly, each CWD type harboured 5-7 unique species, i.e. some species were solely found in stumps, while others were only seen in snags or in logs.

Boulanger and Sirois (2007) described two phases of saproxylic insect colonization of fire-killed black spruce. The first, composed mainly of rapidly-dispersing phloem and xylem feeders targeting snags, occurred very soon after the death of the trees. These initial populations slowly declined (with no species replacement) as the moisture content was reduced to a point where decomposition rates became negligible (Boulanger and Sirois, 2006). A second colonization phase was detected once the snag fell to the ground at which time the moisture content and rate of decomposition increased substantially favouring fungivores and epigaeic saprophages (Boulanger and Sirois, 2007). The time for a tree to fall after death is on average about 5-20 years in North America; but this right skewed distribution of time-to-fall can include some snags that remain standing for 50 years (Johnson and Greene, 1991). Decomposition is quite slow until the snag lies on the ground.

The relationship between FWD and invertebrates has been much less studied, primarily because it was assumed that CWD was a far more important substrate for almost all saproxylic species. However, recent work suggests that some species of saproxylic invertebrates may be associated specifically with small-diameter woody material (Jonsell, 2008a). Jonsell et al. (2008b) reported that up to 22 of the red-listed saproxylic beetle species in Scandinavia were found in logging residue and of the 160 beetle species captured, 35 were associated with a specific diameter class, including in some cases FWD.

In summary, species richness and the abundance of invertebrates are influenced by the physical characteristics of their habitat, many of which are altered by biomass harvesting. The presence of coarse and fine woody debris provides structural heterogeneity that in turn contributes to the maintenance of a large number of physical attributes (e.g. variable sun exposure, moisture and shelter opportunities) as well as providing food for saproxylic invertebrates. In addition, changes in these physical attributes affect meta-population dynamics by fragmenting habitats at the scale of the cut-block and at larger spatial scales. Considering the wide variability in dispersal potential between invertebrates as well as the varied habitat preferences, it is difficult to accurately predict the effects of slash removal (Jonsell, 2007). Quantitative predictions require knowledge of the local- and regional-scale processes, and these are lacking. Time and money constraints have made such studies essentially impossible; the logistical problems are compounded by the relative small number of scientists interested in non-pest invertebrate diversity in relation to forestry practices. Jonsell (2007) pointed out that even what we do seem to know is often based on unrealistic work: E.g. most studies concerning the effects of FHR removal evaluate extremes: no slash vs. slash. In reality, as pointed out earlier, contemporary WTH operations do not remove only about half of the logging residue. Nonetheless, to insure that invertebrate biodiversity is maintained, Kappes et al. (2009) in central Europe suggested that a minimum of 9 t/ha of slash be left on-site (although this value is little more than an educated guess). Recent recommendations suggest a minimum of 20 m^3/ha (Work and Hibbert, 2011). However, none of the recommendations give a suggested spatial pattern for these 20 m^3/ha of slash; studies on the effects of the spatial distribution of slash are needed.

An imaginary situation where all dead wood is removed could certainly lead to local and, possibly, regional extinctions of the most obligate saproxylic species, a situation partially observed in parts of Scandinavia where dead wood management has only recently been introduced (Siitonen, 2001; 2011). While FWD on the ground may not be as important as FWD in living trees and small and large CWD on the ground (Ferro, 2009), conclusions are yet to be made, so it may be wise to leave a minimum of 20 m^3/ha of CWD on site, in a variety of spatial arrays.

Objectives and dissertation structure

While this dissertation consists of three empirical studies, I nonetheless develop the concept that because of the many competing "uses" for slash discussed above, forest harvest residue is best regarded as a management tool. In particular, one can imagine the day when a timber harvest proposal is associated with a slash management plan that details how much slash to remove for energy use and how much -and in what distribution- to leave on site as a resource to particular groups of organisms and to sustain ecological functions, while remaining economically viable.

The three chapters in this dissertation examine how slash aggregation affects soil fertility, plant growth, plant reproductive output, and plant juvenile survivorship. All three studies (except part of the data in Chapter 1) were within a km of each other in a pair of recent clearcuts in the Riviere-aux-Rats (RaR) region in the Mauricie of Quebec. In each case, the substrate was a sandy loam (classified as a Humo-Ferric Podsol), and it was hypothesized that one would see nutrient augmentation near aggregated slash.

The first chapter examines how large aggregations of woody residue (slash piles) affect soil fertility and the growth of plants. Using transects radiating away from two arrays of piles at the same harvest block, gradients in soil fertility, growth of early-successional plant species, and their reproductive output (flowers and fruits) were measured. Chapter 2 reports on a study at the same harvest block but with the focus on the growth of the planted hybrid poplars. In particular, the law of constant final yield is used to demonstrate that the faster growth of poplars near piles is due to augmented soil nutrients rather than to the extra available light above piles (the same light level available everywhere in the young plantations). The final chapter uses a gradient of loadings from about 0 to 60 kg/m^2 green mass to test the hypothesis that an intermediate loading of slash will lead to the highest juvenile survivorship for two sown tree species. That is, the tested argument was that at very low loadings survivorship of small seeded tree species will be poor because of soil drying whereas at very high loadings the aggregated wood will physically prevent the seed from reaching the underlying substrate.

The dissertation ends with a global conclusion.

CHAPITRE I

THE ROLE OF AGGREGATED FOREST HARVEST RESIDUE IN SOIL FERTILITY, PLANT GROWTH, AND POLLINATION SERVICES

[ARTICLE in SOIL SCIENCE SOCIETY OF AMERICA JOURNAL · JANUARY 2014]

1.1 Abstract

While post-harvest residue ("slash") is increasingly viewed as a source of biofuel, few studies have considered the potential ecological impact of the spatial distribution of forest harvest residue. We hypothesized that slash piles create islands of high soil fertility and light, leading to greater abundance, growth, and reproduction of plants. In 6-yr-old intensively managed hybrid poplar (*Populus balsamifera L. P. maximowiczii A.* Henry) plantations, we showed that soluble organic N, NO_3–N, NH_4–N, and P decreased as a negative exponential function with distance from the pile. Pin cherry (*Prunus pensylvanica L.* f.) relative growth rate was fastest near piles in the first few years after harvest. We found significantly greater stem size, flowers per plant, and foliar P near piles for cherry, and this inverse gradient sharpened in a 16-yr-old white spruce [*Picea glauca* (Moench) Voss] plantation. For the two other flowering species, strawberry (*Fragaria virginiana* Mill.) and raspberry (*Rubus idaeus* L.), flower and fruit abundance were also significantly and strongly negatively correlated with distance to the pile. Further, directly correlating soil nutrient availability with plant traits, we found significant positive relationships between plant growth, reproductive output, and N availability. Partial correlation analysis indicated that more of the variance in plant traits was explained by distance than by soil nutrition. We conclude that in industrial forests, piles replace canopy gaps as sites where understory plant species can episodically reproduce and are therefore important for many plant species as well as the pollinators and frugivores dependent on them.

1.2 Introduction

Many primary and secondary ecosystem services such as soil fertility, water filtration, and food resources associated with the pollination of fruiting plants are dependent on the management and maintenance of ecological processes and function in forests (Flaspohler and Webster, 2011; Schröter et al., 2005). Management of deadwood, in particular, with its effects on soil fertility and species abundance and diversity, has recently become an important issue in sustainable forest management (Evans et al., 2013; Spence, 2001). Many recent studies and reviews have evaluated the effect of slash or fine woody debris (FWD) on soil (Johnson and Curtis, 2001; Thiffault et al., 2011) and biodiversity (Bunnell and Houde, 2010; Riffell et al., 2011), and several have examined the effects of the spatial distribution of slash on vertebrates and invertebrates that use downed wood as habitat or for nesting (Bunnell and Houde, 2010). However, we have not found a single study that investigated the effect of aggregated slash on the abundance and presence of flowering plants or the importance for dependent pollinator invertebrates and frugivores.

Likewise, few studies of soil fertility or plant responses have differentiated between FWD left as discrete piles and windrows and residue more uniformly distributed over the cut block. Although the literature on the effect(s) of FWD on soil fertility is indeterminate (Johnson and Curtis, 2001; Laudon et al., 2011), it is becoming clear that removal of FWD depletes soil fertility on sandy sites in the middle to long term (starting around 15 yr) in the mid-latitudes (D'Amato et al., 2012). Given that soil nutrients may vary markedly at the meter scale (Jackson and Caldwell, 1993) and, as shown here, that effects of piles on soil fertility may extend only a few meters from the edge, spatially explicit studies of the effect of FWD on soil nutrient availability are needed. Studies that compare only different blocks with or without slash, or that compare blocks with slash remaining as piles vs. those where slash is distributed uniformly, will be problematic because the spatial distribution should have quite different effects on the soil nutrient status and plant yield and diversity.

The spatial pattern of post-harvest residue becomes especially important when considering its effects on species competing with the planted crop. One expects uniformly distributed slash to enhance nutrient availability more evenly, and for a shorter period of time, than piles or windrows because a much larger percentage of the wood is in contact with the ground. For example, Morris (2009) found increased concentrations of dissolved organic N (DON), soluble organic N (SON), and soil organic N following distribution of chipped wood across a harvested plantation area than without the chipped wood. However, an even distribution will not delay canopy closure anywhere within the harvest block as the crop grows. By contrast, piles and windrows will release nutrients more slowly and enhance available light by locally delaying canopy closure of the planted species. In short, flowering plants should be more abundant and vigorous on or near discrete collections of slash where light and soil nutrient availability are greatest.

In the mid- to high latitudes, trees are predominantly wind pollinated and wind dispersed; by contrast, the understory is predominantly composed of shrubs and perennial herbs pollinated and dispersed by animals (Daubenmire, 1968; Regal, 1982). These zoophilous fruit-bearing shrubs and herbs will typically only have adequate resources for sexual reproduction in recent canopy gaps, that is, where light is abundant. In the eastern hardwood–boreal transitional forests of North America, such gaps are episodic and due primarily to high-magnitude wind or ice events (Pickett and White, 1985). However, in short-rotation (10–30 yr), intensively managed plantations grown for biofuel or pulp, canopy gaps will be rarer because stress risers (for example areas of fungal rot where wood fibers are no longer interconnected and thus incipient cracks develop) will not have had time to develop (Niklas, 1992) and very small trees will bend rather than break when heavily loaded with snow or ice (Proulx and Greene, 2001). Although stocking failure, a possible source of small-scale gaps, has been a problem in the past, in the more recent plantations of eastern Canada, survival of planted stock is about 95% (Arbec, personal communication, 2013). In summary, in intensively managed stands, piles and windrows may be the principal source of enhanced light as canopy closure ensues and a simple way to partially emulate the natural disturbance regime in managed forests.

Further, due to the higher available light and nutrients, we expect plants near or on discrete patches of woody residue to grow faster than conspecifics elsewhere in the cut block. It is well understood, especially with cultigens grown for fruit production that faster growth leads to an earlier onset (precocity) of sexual function (Thomas, 2011). Given equal age, at all sizes, bigger plants will both reach sexual maturity earlier and produce more flowers and fruits annually than will smaller plants (Greene and Johnson, 1994; Meilan, 1997; Shipley and Dion, 1992; Zimmerman, 1972). Soil nutrient status, and P in particular, is known to play a role in both the induction and intensity of flowering and subsequent fruit output (Neilsen and Yorston, 1991). In this way, piles differ from natural canopy gaps in that they represent a long-term source of elevated soil nutrients.

Using intensively managed plantations of hybrid *Populus* spp. and *Picea* sp. growing on sandy till in eastern Quebec, we investigated how the presence of discrete piles of post-harvest wood residue influenced the spatial distribution of available soil nutrients and the distribution, growth, and reproductive output (flower and fruit) of early successional flowering plants. We hypothesized that piles functionally replace canopy gaps in intensively managed forests by providing "hotspots" of resource availability conducive to the early success of flowering plants. We expected that competing plants close to slash piles and windrows will grow faster, reach reproductive status earlier, and account for a dramatically larger fraction of the flowers and fruits than conspecifics found farther away from piles.

1.3 Methods

1.3.1 Study Sites

To evaluate soil fertility, growth, and reproductive output of fruiting plants with distance to a pile, we used a 6-yr-old hybrid poplar plantation on a sandy loam site at Riviere-aux-Rats (RaR), in the Goulet sector of the Haute Mauricie region of Quebec (47.292 N, 73.038 W). In addition, we evaluated the growth and reproductive output of cherry (but not soil fertility) on a sandy till at Zec Owen in a 16-yr-old spruce plantation in the Temiscouata region of Quebec (47.837 N, 68.477 W). These two areas have short, 5-mo growing seasons and long winters; the mean temperature is 2° C. Precipitation is about 900 mm annually, with 30% falling as snow. The preharvest canopy was a mix of 20-m-tall, closed-canopy white and black spruce [*Picea glauca* and *P. mariana* (Mill.) Britton et al.], balsam fir [*Abies balsamea* (L.) Mill.], balsam poplar (*Populus balsamifera* L.) and yellow and paper birch (*Betula alleghaniensis* Britton and *B. papyrifera* Marshall).

The RaR site was whole-tree harvested, with delimbing and piling at the roadsides, and the sites were prepared with 1-m mounding in 2005. Hybrid poplar stock was planted using 2- by 2-m spacing. Competing woody stems were treated with brush-sawing in 2007 to 2008, as *Prunus* stems (and other competitors) are cut if there is any reason to think the focal species may not achieve free-to-grow status (when competing individuals are within 2 m and >2/3 the height of the commercial planted species) (Gouvernement du Québec, 2008). We note that competition elimination was as intense near as far from piles; essentially all *Prunus* stems that we examine in this paper were asexual recruits sprouting from sawn root collars.

1.3.2 Experimental design

At RaR, there were two arrays of piles. The two arrays each had 6 piles, the arrays about 300 m apart. Within each array, the 6 piles were about 20 m apart and had volumes of about 200 to 500 m^3 (including air space). The piles at one array were a curving line, somewhat perpendicular to the contour (referred to hereafter as the upslope array), while the piles at the second array were a row along the contour further downslope (referred to from now as the downslope array). The piles were composed completely of harvested material and their upper surfaces showed no evidence of decomposition; for example, bark remained on the boles and branches. The windrows at the older Zec Owen site, again derived from the initial harvest of trees, were in an advanced stage of decomposition; the upper branches and boles could not be identified to species, and sexually recruited plants were now growing on top of the piles. The Zec Owen windrows were parallel and about 30 m apart, and typically about 5.5 m wide and 2 m high.

At RaR, we used one to (more typically) three transects radiating away from the slash piles to collect data on soil and plant attributes for a total of 31 transects. The only exception was cherry basal area, for which we sampled all cherry stems within 20 m of any of the 12 piles. We measured the cherry basal area and soil status at RaR in 2011, with soil sampled at distances of 0, 2.5, 5, 9, 14, and 20 m from the pile, deliberately sampling more intensively near the piles. When the 14- and 20-m distances were within 12 m of another pile, those data were not used (to avoid multiple distance effects). The flowering of raspberry and strawberry, and the fruiting of the former, were measured in 2012 at RaR. Cherry flowers were sampled along a total of eight transects in 2013. In 2013, we measured the size and reproductive output of cherry along eight transects in the 16-yr-old spruce plantation at Zec Owen.

1.3.3 Soil Fertility and Foliar Nutrition

In late August 2011, a total of 190 resin bags (39 at 0 m, 40 at 2.5 m, 35 at 5 m, 27 at 9 m, 26 at 14 m, and 23 at 20 m) were placed at the 10-cm depth in the soil along the RaR transects. Holes were dug manually, using fingers, to avoid compaction and to remove any sharp stones adjacent to the bags. The bags were left in situ for approximately 10 weeks and recovered in early October 2011.

Ion-exchange resin bags (Binkley et al., 1992) were constructed using 20 g of mixed-bed ion-exchange resin (J.T. Baker JT4631^{-1}) and secured with nylon ties inside sections of beige and black nylon stockings (Secret 5837Y) and regenerated with 1 mol L^{-1} HCl. Upon retrieval, the resin bags were kept cool in sealed plastic bags while en route to the Canadian Forest Service (CFS) laboratory in Quebec City. Resin bag contents were extracted in2 mol L^{-1} KCl and colorimetrically analyzed for NH_4–N and NO_3–N concentrations using a Lachat Instrument automated ion analyzer. In early October 2011, 220 mineral soil core samples were collected to a depth of 15 cm using a 5-cm-diameter by 15-cm polyvinyl chloride corer at the same distances and along the same soil transects as were used for the resin sampling. In a few places, where it existed, an organic layer was collected separately. Of these 220 mineral soil samples, 75 were selected and prepared for laboratory incubation to measure N mineralization rates, and another 55 were ground for mineral content determination. Soil texture of the sandy loam was determined by granulometric analyses (Carter, 2007) and the moisture percentage was measured. The soil was characterized as a Humo-Ferric Podzol using Soil Classification Working Group (1998).

We used a 6-wk aerobic laboratory incubation at room temperature to evaluate net N mineralization and nitrification potentials (Hart and Binkley, 1985). Net N mineralization and net N nitrification were estimated as the difference between the pre- and post-incubation amounts of NH_4–N and NO_3–N extracted with KCl. Soluble organic N was determined by subtraction of the quantity of mineral forms of N from the amount of NO_3–N present following persulfate oxidation (Cabrera and Beare, 1993).

The air-dried, <2-mm soil core samples were analyzed for pH, total N and C, exchangeable Ca, Mg, and K, and P by the CFS Soil Analysis Laboratory. Exchangeable cations (Al, Ca, Mg, Mn, and K) were extracted with an unbuffered Mehlich III extraction solution and measured using inductively coupled plasma emission. Soil pH was measured in water using a soil/solution ratio of 1:2.5, and total C and N were determined on a Leco CNS 2000 analyzer (Carter, 2007).

1.3.4 Foliar Analysis

Prunus foliar samples (n=35) were collected at the upslope pile array, using the same 20-m soil transects but now extending them out to 30 m from the piles in mid-August 2011. Ten leaves were collected from the topmost sun leaves (the smaller, more dissected leaves in the upper crown) of the canopies. The foliar samples were placed in small paper bags and kept moist for 7 h while en route to the laboratory, where they were immediately dried in an incubator at 55°C for 72 h and their dry mass measured. Concentrations of C and N were analyzed on a Leco CNS-2000. A subsample was ashed at 500°C and the ash recovered in 1 mol L^{-1} HCl (Kalra, 1998, p. 53–56). Phosphorus and cation concentrations were determined by inductively coupled plasma analysis (PerkinElmer Optima 7300DV).

1.3.5 Growth and Reproductive Output

We examined the growth and sexual response of three fruiting species. Pin cherry (bird cherry, wild red cherry, or fire cherry) is an endozoochorous shade-intolerant tree that reproduces both sexually and asexually, has a long seed dormancy of many decades, provides important floral and fruit resources to wildlife, is dispersed by many birds and mammals (Jobidon, 1997; Marks, 1974; Nyland et al., 2007), and typically flowers (and fruits) only in gaps (Collins and Pickett, 1988; Marks, 1974). Its small flowers emerge from buds in the early spring and are insect pollinated (Grisez, 1974). The resulting fleshy red drupe is about one-fourth the size of domestic cherries and ripens in midsummer in this region. Although fruit production is variable, with large crops having a periodicity of 3 or so yr (Marks, 1974), by contrast, flower production is more constant from year to year (Guittian, 1993; Stephenson, 1981). Pin cherry has a shallow root system, with most roots occurring within 60 cm of the soil surface (Grisez, 1974), and is highly efficient at taking up NH_4–N; indeed, the absence of the nitrate reductase enzyme in cherry precludes the uptake of NO_3–N (Truax et al., 1994).

Raspberry is an intolerant, nitriphilic understory shrub (Donoso and Nyland, 2006; Jobidon, 1993; Truax et al., 1994), highly valued for its fruit by wildlife (Howe et al., 2012; Marks, 1974). In June and July, *Rubus* produces copious flowers of dilute nectar attractive to many long-tongued pollinators such as *Osmia* and *Bombus* sp. (Whitney, 1984), which are, if pollinated, followed by large crops of sugar-rich red berries in July and August. Its persistence is dependent on canopy gaps and its regeneration is aided by long-term soil seed dormancy (Whitney, 1984).

Strawberry, common across North America, is a small gynodioecious herbaceous plant, producing white flowers in late May in this region and, following pollination by small bees and flies, small red berries in June (Ashman et al., 2005).

Our measure of plant size was basal area (cross-sectional area 2 cm above the soil) for cherry, and number of leaves m^{-2} for raspberry and strawberry. Cherry stems everywhere at RaR were of the same age and were >1 m in height (our minimum for sampling). The basal area of each cherry within 20 m of a pile was calculated as the sum of the basal areas of each stem arising from the root collar. There was an average of 2.7 stems per clone. Recent sexually derived stems occurring on slash piles were common at Zec Owen; at RaR, sexually derived stems were often too small to be included in the analysis. For cherry flowering in 2013, we used transects radiating from the piles and measured the basal area of all clonal stems. In the older spruce plantation, cherry basal area and flowers per clone were measured in 2013 along 20-m transects extending at a right angle from the two windrows.

In 2012, in contiguous 0.2-m² (0.4 by 0.5 m) quadrats along the soil transects, we measured the number of raspberry and strawberry leaves, flowers, and (raspberry only) fruits. For a subset of quadrats, we took 10 raspberry fruits and leaves (fewer if there were less than 10 available), dried them, and then measured their mean mass. For the plant soil correlation analyses, we summed four vegetation quadrats per soil sample plot. For example, at 0 m from a pile, we examined plant traits in relation to soil measures for vegetation quadrats 0 to 50, 50 to 100, 100 to 150, and 150 to 200 cm; at 2.5 m from a pile, we included vegetation quadrats 200 to 250, 250 to 300, 300 to 350, and 350 to 400 cm.

To test our hypothesis regarding early success of cherry due to higher NH_4–N availability in early years near piles relative to far from piles, we cut at the base the largest clonal stem of 16 cherry trees near piles and far from piles at the upslope pile array at RaR. For each, we measured the ring width on three lines from pith to bark. Using the average annual ring widths and total diameter for each stem, we calculated the relative growth rate (RGR) for each year as (Causton, 1977)

$$\mathrm{RGR} = \ln W_2 - \ln W_1 / (t_2 - t_1)$$

where W_1 is the tree's diameter in year t_1 and W_2 is the larger diameter 1 year later (t_2).

We examined the growth and sexual response of three fruiting species. Pin cherry (bird cherry, wild red cherry, or fire cherry) is an endozoochorous shade-intolerant tree that reproduces both sexually and asexually, has a long seed dormancy of many decades, provides important floral and fruit resources to wildlife, is dispersed by many birds and mammals (Jobidon, 1997; Marks, 1974; Nyland et al., 2007), and typically flowers (and fruits) only in gaps (Collins and Pickett, 1988; Marks, 1974). Its small flowers emerge from buds in the early spring and are insect pollinated (Grisez, 1974). The resulting fleshy red drupe is about one-fourth the size of domestic cherries and ripens in midsummer in this region. Although fruit production is variable, with large crops having a periodicity of 3 or so yr (Marks, 1974), by contrast, flower production is more constant from year to year (Guittian, 1993; Stephenson, 1981). Pin cherry has a shallow root system, with most roots occurring within 60 cm of the soil surface (Grisez, 1974), and is highly efficient at taking up NH_4–N; indeed, the absence of the nitrate reductase enzyme in cherry precludes the uptake of NO_3–N (Truax et al., 1994).

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$$\mathrm{RGR} = \ln W_2 - \ln W_1 / (t_2 - t_1)$$

where W_1 is the tree's diameter in year t_1 and W_2 is the larger diameter 1 year later (t_2).

1.3.6 Statistical Analysis

T-tests of log values of soil or cherry leaf attributes or cherry wood volume indicated no significant differences (p ranging as 0.13 to 0.78) between the two arrays of piles despite the fact that one set of piles was along contours and one set perpendicular to the contours. Likewise, within the latter array, perpendicular to the contours, ANOVA showed no discernable effect of the piles (p ranging as 0.24 to 0.86). We also found no differences due to transect direction (north vs south; east vs west) using t-tests of log-transformed values (p ranging as 0.21 to 0.90). Subsequently therefore, data from the two pile arrays and transects were combined, and in all subsequent statistical treatments we used Pearson product moment correlations of the transect-averaged values because we no longer had reason to explicitly treat the effect of an individual site or pile as a fixed effect.

We used semi-logarithmic correlational analysis because we found that the sharply curvilinear data could best be represented by a logarithmic transformation of the attributes as a function of distance to the pile. Finally, because there was a tendency for both soil and plant attributes to asymptotically flatten at distances of about 8 to 15 m from a pile edge, correlations were based solely on the subset of data at distances of 12 m or less from a pile edge.

When directly comparing plant traits (every 0.5 m from the pile to as much as 30 m away) with soil measures (located at distances of 0, 2.5, 5, 9, 14, and 20 m), we averaged the former before performing correlations. (For example, a plant measure such as strawberry flowers per m^2 in the consecutive quadrats from 7 to 11.5 m along each transect would be averaged for comparison with the fertility measure found at 9 m.) Necessarily, the sample sizes were smaller than before because (i) we had to average the plant trait observations to correspond to the six distances used for each soil transect, and (ii) plant traits were measured only on a subset of the piles used for soil measurements. We excluded plant data for distances >23 m (because we almost invariably had zero values for fruits and flowers at such great distances). We found that in the majority of cases (64% of the 110 cases in Tables 1.2 and 1.3), log–log correlations were superior to semi-log regressions for these markedly curvilinear data.

Finally, to disentangle the inter-correlation of soil attributes and distance from the pile on plant attributes, we performed partial correlation analyses that held, alternately, either the soil attribute or distance constant as we examined the role of the remaining variable in determining plant responses. Necessarily, values for plants were constrained to the same distances where the soil had been sampled.

1.4 Results

Results from the correlation analysis are given in Tables 1.1 to 1.3, with selected examples of the more important relationships (distance from the pile and plant and nutrient attributes) presented in the Figures.

1.4.1 Soil Nutrients in Relation to Distance to Pile

There was no discernible mesic organic horizon at distances >5 m from a pile. At lesser distances, only five measurable organic layers were present out of a possible 249 samples.

Semi-logarithmic correlations from 0 to 9 m from pile edges for soil resin bag results showed inverse and significant relationships for the sum of major base cations, as well as for NH_4–N, NO_3–N, and P (Table 1.1; Figure 1.1). For the N laboratory incubation, SON and NO_3–N, but not NH_4–N, showed a significant negative correlation with distance from a pile (Figure 2.2).

Of the soil measures examined in the mineral core analyses, none showed a significant effect of distance from a pile (Table 1.1). Moisture content (%) was also not correlated with distance.

With the foliar analyses for cherry (conducted solely at the upslope array), only P showed a significant (and inverse) distance-related effect (Table 1.1).

1.4.2 Plant Size as a Function of Distance to Pile

Plant size (basal area or leaves per square meter) also showed a negative relation with distance from a pile (Table 1.2). Cherry basal area (m^2) at RaR had a weak but inversely significant relationship with distance from a pile (Table 1.2). Cherry mean dried leaf mass per tree was significantly and inversely related to distance from a pile; i.e., the leaves tended to be larger farther from piles.

The number of raspberry leaves per square meter showed a strong negative relationship with distance (Table 1.2; Figure 1.3). Note that with raspberry at RaR, unlike cherry or strawberry, the first 2 m represent raspberry on the pile itself. The raspberry found on the piles at RaR were all horizontal extensions of shoots from near the pile edges.

The strongest significant inverse relationship was (unlike cherry) between individual leaf mass and distance; raspberry leaves were not only more common near piles but also tended to be bigger.

By contrast, strawberry leaves per square meter showed no significant relationship with distance; the modal distance was a few meters away from the pile edge

(Table 1.2; Figure 1.3). Generally, strawberry plants were never found under the shade of raspberries or other shrubs, especially at distances <2 m from a pile, where shading by shrubs was most intense.

The effect of pile proximity on plant size was more apparent in the 16-yr-old plantation at Zec Owen (Figure 1.3). There, the cherry trees growing near and (like raspberry at RaR) on slash piles showed a much stronger relationship between basal area and distance from the pile than at the much younger stand at RaR (Table 1.2). Further, the slope of the semi-log relationship was significantly steeper at Zec Owen than at RaR (t -test, $p < 0.0001$). Note that unlike in the younger plantations, several cherry trees were growing on the piles themselves, and thus in the correlations, the edge of the pile is at approximately 2.3 m. Although not quantified in this study, raspberry plants at Zec Owen were limited almost completely to the piles themselves and the edges, where they were a mix of sexual and (horizontally spread) asexual stems. As for strawberries, very few were noted at Zec Owen.

1.4.3 Plant reproduction in Relation to Plant Size and Proximity to Pile

Flower and fruit production were strongly related to plant size. At RaR, log–log correlations within 12 m of pile edges showed that cherry flower abundance was significantly (and positively) correlated with basal area (Table 1.2). Likewise, raspberry flowers or fruits per square meter were correlated with leaves per square meter. For strawberry, flowers per square meter was also significantly correlated with leaves per square meter. For cherry flower abundance at the older 16-yr-old plantation, the relationship between reproductive output and basal area was highly significant (Table 1.2).

The flowers or fruits of the three species were found mainly near piles. At RaR, a semilog regression for cherry flowers on distance was significant (Table 1.2; Figure 1.4). At the Zec Owen site, the same effect was far more pronounced; 93% of all flowers were produced by cherry growing on or within 2 m of a pile (Table 1.2; Figure 1.4).

For raspberry flowers and fruits, all semi-log correlations with distance were significant and inverse (Table 1.2; Figure 1.4). Likewise, the mean dried fruit mass of raspberry decreased with distance.

Finally, for strawberry flowers (unlike strawberry leaf density), there was a significant inverse effect of distance (Figure 1.4). The modal distance, however, remained a few meters away from the pile edge.

A measure of reproductive efficiency, the density of fruits or flowers per density of leaves or per basal area (cherry) showed declines with distance for all species (Table 1.2). At the RaR site, cherry had a strong relationship between flowers per basal area and inverse distance from a pile. Likewise, the ratio of strawberry flowers per leaf was significantly and inversely proportional to distance (Figure 1.4). For raspberry, the ratios of the density of fruits or flowers (Figure 1.4) to leaf density both yielded significant correlations. Likewise, the ratio of dried fruit mass to dried leaf mass declined significantly with distance. At Zec Owen, the relationship between cherry flowers per basal area and distance to a pile was far stronger than at the younger RaR plantations. Additionally, the slope of the semi-log regression for cherry was significantly steeper at the older Zec Owen plantation.

1.4.4 Reproductive Performance and Plant Size as a Function of Soil Nutrient Status

Log–log correlations of plant traits with direct measures of nutrient availability from resin bag and N incubation analyses at RaR (Table 1.3) generally showed that distance was better correlated with plant traits than were soil nutrients measured from resin bags (Table 1.3 vs. Table 1.2). By contrast, soil incubation measures (Table 1.3) tended to be almost as well correlated with plant traits as distance, and the correlation between NH_4–N and cherry growth (Figure 1.5) was far higher than between NH_4–N and distance from a pile.

Because the modal density of strawberry leaves was well away from the pile edge, there was no significant correlation with any resin-based soil variable, and the positive correlation between strawberry flower density and P was the only significant result (Table 1.3). By contrast, using the N incubation results, both NO_3–N and SON (but not NH_4–N) were positively correlated with measures of strawberry performance.

Raspberry foliar and reproductive attributes showed a number of positive, significant correlations with resin soil measures. Concentrations of NO_3–N were significantly correlated with all size and reproductive traits except for fruits per leaves and fruit mass per leaf mass (Table 1.3). Concentrations of NH_4–N and P each showed two significant positive relationships. Incubation results for N_{O3}–N and SON were positively correlated with all raspberry measures except those involving mass. For the non-mass plant traits, NH_4–N tended to be negatively correlated but was not quite significant (Table 1.3).

For cherry, both flowers per basal area and flowers per tree were significantly and positively associated with soil NO_3–N from the resin bag analysis (Table 1.3). The ratio of flowers to basal area was also significantly correlated with NH_4–N. Turning to the incubation results, SON was significantly (positively) correlated with all three cherry measures, while NO_3–N was significantly and positively correlated only with flowers per tree. Concentrations of NH_4–N were significantly (positively) correlated with cherry basal area.

With partial correlation analysis using the seven soil and 15 plant attributes (Table 1.3) and the distance vs. soils data (Table 1.2), we found that distance (which includes all potential effects aside from soil nutrition) had a higher partial correlation with plant responses than did soil nutrition alone (Table 1.3). Distance had significant ($p < 0.05$) partial correlations in 87 of 105 cases and soil nutrition considered alone in 17 of 105 cases (Table 1.3). Averaging across the 105 examples, distance explained 24% of the variance in plant traits, whereas soil factors considered alone explained on average 6%.

1.4.5 Cherry Growth Rates in Relation to Distance to Pile

Only two disks displayed a ring for 2006; therefore those two rings were omitted. Dividing the trees into those near (<4 m) or far (>4 m) from a pile, we find that relative growth rates (RGR; Figure 1.6) have been similar. In both cases, RGR is declining with time, presumably because the planted poplars had started growing rapidly and thus more shade is being cast on the cherries.

1.5 Discussion

We found a significant soil fertility gradient, declining with distance from piles, especially for N. Similarly, concentrations of NO_3–N and SON, and to a somewhat lesser extent soil P and NH_4–N, were significantly correlated with plant traits. To our knowledge, this is the first study to show a direct correlation between soil NH_4–N and cherry growth (Figure 1.5) and flower output and between soil P and flowering in *Rubus* and *Fragaria* under field conditions. Finally, and most strongly, growth and reproductive output of the three flowering and fruiting plant species declined with distance from the piles, and this effect was especially strong at the older 16-yr-old plantation.

The greater light above and near piles, although not measured in this study, undoubtedly augmented the soil effects on plant performance (Wender et al., 2004). A strong light gradient at RaR from the pile edge to approximately 7 m is inferred because the growth of poplars was far greater near piles (data not shown). Partial correlation analysis was used to separate the effects of soil nutrients on plant attributes from other factors, which notably would include light but also other factors not measured in this study. Partial correlation analysis held either distance or soil factors constant and showed that distance explained more of the variance in plant attributes than soil nutrients. At first glance, the difference in explanatory capacity (the r2) can be viewed as representing the contribution of light and other factors to the effect of distance to a pile on plants, but fertility measures are extraordinarily variable even at a spatial scale of a few meters (Jackson and Caldwell, 1993). Furthermore, the relationships between soil and plant attributes do not take into consideration the full soil volume explored by roots; because roots are known to extend toward zones of high nutrient availability, and presumably near piles, this could diminish slightly the explanatory power of soil–plant attributes relationships. Interestingly, when plant traits were regressed on soil incubation measures, the correlations were much higher on average than with the resin results, especially those between plant performance and incubation N.

1.5.1 Soil Fertility

Soil nutrient availability decreased with distance from a pile, especially for P, NO_3–N, and NH_4–N. This result can be compared with studies that evaluated sandy sites with and without slash because the far ends of transects in our study can be considered as a "without slash" treatment. Ballard (1978), in a spatially explicit study of Radiata pine (*Pinus radiata* D. Don) growing on a pumice soil, found increased soil N, foliar N, and tree growth on and near windrows, and some recent studies on the effects of FWD removal, such as D'Amato et al. (2012), reported a decrease in NO_3–N and overall soil fertility on sandy sites after 15 yr. Harrington et al. (2013) saw an increase in seedling growth, soil water, and foliar N under higher loadings of slash.

While much of the lack of unanimity among previous studies can be attributed to soil, site, or treatment differences (Fox, 2000; Johnson and Curtis, 2001; Reich et al., 1997; Thiffault et al., 2011), some of it is probably due to three methodological differences. First, most studies evaluating site productivity at the stand level have not sampled intensively along a spatial gradient, especially close to piles. Instead, these studies tended to sample only near piles, or they have compared blocks where slash has been removed with those with slash remaining but without specifying the spatial distribution of the slash or where sampling plots were located in relation to piles or windrows (Eisenbies et al., 2005; Johnson and Curtis, 2001; Thiffault et al., 2011). Second, the typically strong heterogeneity among soil attributes at small spatial scales (Jackson and Caldwell, 1993; Reich et al., 1997) will produce statistical significance only with a very large sample size (Johnson and Curtis, 2001). Finally, previous investigations (with different research goals) have perhaps sampled sites too soon after harvesting, whereas it is likely that differences in soil nutrient availability become apparent only after a few years (Ballard, 1978; Thiffault et al., 2011), particularly where slash was left as piles rather than uniformly distributed.

Phosphorous, an important mineral in rooting and the induction of early flowering (Neilsen and Yorston (1991) as well as for subsequent flowering intensity (Erel et al., 2008), was found in significantly higher amounts near piles (resin analysis) as well as in cherry leaves. Further, soil P availability was directly correlated with plant reproductive output (flower and fruit abundance). Similarly, soil NH_4–N and NO_3–N as well as SON tended to decline significantly with distance. While soil nutrients clearly influence plant growth, plants can also affect soil fertility. For example, soil NO_3-N in the resin-bag study tended to show a stronger inverse gradient with distance to a pile than did NH_4-N. This may be because near-pile precocious cherry trees with their limited capacity to induce foliar nitrate reductase, the enzyme that permits NO_3-N assimilation (Truax et al., 1994), take up significant amounts of NH_4–N (as shown by the strong positive correlation between cherry growth and NH4–N via incubation: Table 1.3; Figure 1.5), thereby potentially reducing the supply of NH_4–N to soil nitrifiers and reducing the amounts of NO_3–N. Despite this reduction in NH_4–N, NO_3–N remained high near the piles; this may be because the piles were large and only 6 yr old, so the system was not yet N limited. The inability of cherry to deplete the near-pile soil of NH_4–N and thereby lower the NO_3–N availability to competitors may allow raspberry to persist on and near slash piles far longer than in natural gaps, as found by Truax et al. (1994).

The observed higher soil SON near piles is probably related to the greater amounts of soil organic matter (SOM) (Powers et al., 2005), there being no surface organic residues at RaR at distances beyond 5 m from a pile. There are three likely reasons for this: (i) initially after whole-tree harvest there is a concentrated amount of leaf litter, branch tips, and FWD at the edge of piles relative to elsewhere; (ii) there is increased leaf litterfall near piles, the decrease in gradients of foliar nutrients and poplar growth with distance from a pile being far steeper than with cherry (unpublished data, 2013); and (iii) there are more herbs and shrubs near piles (Table 1.2), which further increases SOM inputs through the fall of litter and berries.

Other studies have demonstrated the importance of understory vegetation in enhancing and sustaining nutrient supply. For example, Polglase et al. (1992) found that removal of herbaceous competition of pines inhibited specific N and P mineralization in a Spodosol in Florida, and Busse et al. (1996) found that the presence of understory vegetation in a ponderosa pine (*Pinus ponderosa* P. Lawson and C. Lawson) stand growing in a sandy loam pumice soil resulted in greater N in the O horizon and upper 4 to 12 cm of mineral soil.

In summary, given the higher near-pile inputs of FWD and organic matter, it is not surprising that N and P availability diminishes

1.5.2 Plant growth and Pile Proximity

An abiding argument against any immediate positive benefit for plant growth from slash or FWD retention is the high C/N ratio of wood. However, FWD and branch tips have a more favorable C/N ratio, as shown by a body of earlier work studying the potential use of fine wood residue as an agricultural fertilizer. This "ramial wood" (defined as FWD between 0 and 8 cm in diameter) has a favorable C/N ratio of 30:1 to 150:1 (vs. 400:1 to 750:1 for stem wood) and has been shown to promote plant growth and yield (increases in strawberry biomass and fruit production of up to 300%: Caron, 1994; Caron et al., 1998). In a more recent study on the use of ramial wood as a fertilizer, Soumare et al. (2002) found increased tomato (*Solanum lycopersicum* L.) foliar N, P, and K concentrations and a 50% yield increase in tomato fruit.

At RaR, pile proximity conferred an early (although weak) growth advantage for cherry, with larger stems and diameter growth rings near the piles than farther away. At the 16-yr-old spruce plantation at Zec Owen, the effect of distance on plant growth was much more pronounced; cherry continued to capitalize on the higher light and soil nutrient availability—via both presumably became more numerous and efficient. Indeed, because of the dense shade of the now closed-canopy spruce, any cherry not on or near a pile was suppressed.

Likewise, raspberry at Zec Owen was noted qualitatively to be restricted to near and on piles and was comprised of a mix of sexual-origin plants and those derived from horizontal movement from asexual-origin plants at the pile edges. As for strawberry, very few plants were found at this site. Initially following a harvest, it is likely that asexually produced and sexually produced weedy plants are common irrespective of distance to a pile, with the former having a tremendous initial growth advantage over the latter. Within 6 yr, however (e.g., RaR), better growth of weedy trees and shrubs is restricted to the vicinity of the piles because of the enhanced light and nutrient availability. For example, we found increased mean cherry foliar mass per leaf far from piles, a typical response to shade. Major and Desrochers (2013) also attributed their finding of increased abundance of fruiting woody species, including *Prunus*, in young stands (6–12 yr post-harvest) and thinned stands (15–16 yr post-harvest) in the same region as our study area to increased light and nutrients. While they did not address location relative to proximity to a slash pile, they found that fruiting species were highly spatially aggregated, especially in unthinned stands. Likewise, Newmaster et al. (2007) found that 5 yr after harvest, the incidence and abundance of herbaceous and woody flowering species in Ontario clearcuts was most positively correlated with slash piles vs. other site treatments. In contrast, short herbaceous species will quickly become limited to those near-pile areas where dense shrubs such as raspberry and fast-growing trees are absent; for example, strawberry was most common at RaR a few meters away from a pile edge. After one to two decades, however, canopy closure leads to the more light-demanding herbs becoming rare everywhere in the block and, as found by Newmaster et al. (2007) or the present study, the shade-intolerant flowering woody species enjoy good growth only very near or on the pile surfaces.

1.5.3 Reproduction of the Competing Plant Species

Reproductive events in plants and pollinators and fruit set are often cued by or dependent on environmental conditions. The control of flowering is extremely important for fruiting plants; for entomophilous or zoophilous species, anthesis must coincide with the presence of suitable pollinators to produce fruit. Temporal and spatial controls on flowering include weather (winter cold: vernalization), day length (photoperiodism), light availability, and soil nutrient status, especially N and P (Erel et al., 2011; Neilsen and Yorston, 1991; Searle and Coupland, 2004). Within a population at a given time and place, however, the main control on the intensity of reproduction is plant size (Shipley and Dion, 1992; Thomas, 2011). Given the positive relationships between propinquity to pile, plant size, and N and P, as well as between size, N and P, and reproductive output, it follows that distance from a pile was also highly correlated with reproductive measures. However, not only did fruit and flower density decline with distance from a pile, but reproductive effort (defined here as reproduction per leaf or basal area) also declined with distance. Indeed, at the older plantation, the fecundity gradient steepened with time since harvest, and reproduction was essentially limited to piles.

This pile-dependent precocity and continued output is important in industrial forest landscapes, particularly for short-rotation hybrid crops. Flowering of understory plants or early successional trees occurs primarily in forest gaps because these, although transient, are the only areas where there is sufficient light and soil resources to sponsor sexual output (Collins and Pickett, 1988; Wender et al., 2004). Natural disturbances such as ice and wind storms can produce large concentrated amounts of downed wood (Krauss et al., 2005; McCarthy et al., 2006), although still far less than what is deposited in a slash pile or windrow. For example, following a 2008 ice storm in Harvard Forest, there was a woody debris input approximately equal to the amount that is normally deposited during a 3-yr period (Munger et al., 2012).

However, with intensively managed plantations such as hybrid poplar, larch (*Larix* spp.), and some fast-growing pine and spruce, the rotation length (<40 yr depending on the crop and the site) is too short for gaps due to natural disturbance to become as common as in a natural forest. This is because there will have been insufficient time for the development of stress risers to enhance stem breakage during wind or icing events (Niklas, 1992; Proulx and Greene, 2001) or the buildup of a large fuel load to increase the probability of fire (Gill and Zylstra, 2005).

Ironically then, slash piles, the undesirable products of whole-tree harvesting, have inadvertently become the major source of high-resource environments for flowering plants in intensively managed plantations. Further, discrete piles of slash are even better than natural disturbance gaps for maintenance of fruiting species (and dependent pollinators and frugivores) because, in addition to the enhanced light, they are concentrated sources of soil nutrients that become rapidly available and remain nutrient sources for a long period, as harvest slash contains short wood pieces and high quantities of FWD (Fraver et al., 2002) of the rapidly decomposing small-diameter classes (Tuomi et al., 2011).

Some non-crop species do not benefit more from an aggregated arrangement of slash. For example, species of mosses or lichens, whose abundance is dependent on the total surface area, will respond better to a more uniform distribution of slash (Newmaster et al., 2007). Likewise, it is thought that some invertebrates, particularly some beetles (Coleoptera), benefit from a dispersed arrangement of slash (Jonsell, 2008); and of course habitat aggregation will test any species' vagility (With and Crist, 1995). However, slash aggregation will increase the abundance and fecundity of some plants (angiosperms and some cryptogams) and animals, especially vertebrates relying on slash for refugia or any animal dependent on flower or fruit resources (Jonsell [2008], Hedin et al. [2008] and McCay [2000] for animals; Newmaster et al. [2007] and the present study for plants).

This study has shown that aggregated slash concentrates soil nutrients and differentially benefits nearby flowering plants and therefore should have positive impacts on the abundance and diversity of pollinators, birds, migratory birds, and other frugivores dependent on them (Cartar, 2005; Major and Desrochers, 2012, 2013). We argue, therefore, that spatially aggregated forest harvest residue may play an important role in the maintenance of biodiversity, especially in intensively managed short-rotation plantation landscapes. In the higher latitudes, in particular, where tree species are invariably pollinated by wind (Regal, 1982), pollinators and frugivores in intensively managed forests will become almost completely dependent on the fruiting plants growing on or near piles.

1.5.4 Policy Implications

These results have potential implications for recent policy issues regarding the removal of slash for use as biofuel. While the removal of slash often confers an immediate commercial reward for woodlot owners and forestry companies and can be a sustainable source of energy, it may lengthen the rotation as this nutrient source is removed (although this extension may depend on the soil and site treatment). At the same time, forest management guidelines have recently recommended minimum amounts of post-harvest deadwood to be left for biodiversity maintenance after forest harvest operations (Dahlberg et al., 2011; Evans et al., 2013; Flaspohler and Webster, 2011; Müller and Bütler, 2010; Weaver et al., 2009) but without consideration of the spatial distribution of the post-harvest residue.

We argue that the spatial arrangement of slash will have important consequences for biodiversity in intensively managed landscapes where natural gaps are rare. Without introducing cost considerations, there are two extreme options for the management of slash: in the first, the slash is uniformly distributed across a block, allowing planting everywhere, which should produce a fast, initial flush of nutrients because most of the FWD is in contact with the soil surface (Morris, 2009). If full stocking is achieved, such plantations will reach canopy closure quickly and thus light-dependent competitors will cease producing flowers and fruit within a few years. At the other extreme, all slash is aggregated in one or several pile(s), within the block or at the roadside. This will lead to a reduction in the area available for planting, a slower release and concentration of nutrients near piles, and large but quite isolated areas where canopy closure is exceedingly retarded.

In this study, we determined that in the longer term the absence of slash piles in industrial forests may decrease the growth and reproductive performance of flowering plants and thus potentially decrease the abundance and diversity of pollinator invertebrates, birds, and mammals. Therefore, guidelines regarding the quantity of deadwood that should be left on site should also consider the spatial arrangement of the deadwood (dispersed vs. piled).

1.6 Tables and figures

Table 1.1. Correlation coefficients of semi-log regressions of soil nutrients on distance from pile. Significant ($p<0.05$) values are bolded.

	C (%)	N (%)	S (%)	P ($g\ kg^{-1}$)	K ($g\ kg^{-1}$)	Ca ($g\ kg^{-1}$)	pH($H_2$0)	Sum of major base cations (cmol(+) kg^{-1})	H_2O (%)	NH_4-N ($mg\ kg^{-1}$)	NO_3-N ($mg\ kg^{-1}$)	SON ($mg\ kg^{-1}$)
Foliar (cherry) (N=78)	-0.179	-0.009	0.050	**-0.397**	-0.047	-0.133	--	--	--	--	--	--
Mineral (N=40)	--	--	--	-0.085	-0.078	-0.158	-0.056	0.010	-0.005	--	--	--
Resin (N=32)	--	--	--	**-0.363**	--	--	--	**-0.446**	--	**-0.529**	**-0.591**	--
N incubation (N=37)	--	--	--	--	--	--	--	--	--	0.084	**-0.394**	**-0.397**

Table 1.2. Correlation coefficients of semi-log correlations of plant responses (size or reproduction) on distance from pile (maximum of 12 m) and of log–log correlations of reproductive traits vs. plant size. Significant ($p<0.05$) values are bolded.

		Independent variable	Correlation	N
Cherry (RaR)	Individual basal area	distance	**-0.179**	233
	Flowers/tree	basal area	**0.712**	60
	Flowers/basal area	distance	**-0.358**	60
	Flowers/trees	distance	**-0.496**	60
	Foliar dried leaf mass	distance	**-0.318**	35
Cherry (Zec Owen)	Individual basal area	distance	**-0.860**	51
	Flowers/tree	basal area	**0.892**	51
	Flowers/tree	distance	**-0.865**	51
	Flowers/basal area	distance	**-0.705**	51
Raspberry	Leaves m^{-2}	distance	**-0.539**	124
	Mean dried leaf mass	distance	**-0.648**	124
	Flowers m^{-2}	distance	**-0.639**	124
	Fruits m^{-2}	distance	**-0.631**	124
	Mean dried fruit mass	distance	**-0.564**	136
	Flowers m^{-2}	leaves/m^2	**0.640**	124
	Flowers/leaves	distance	**-0.585**	124
	Fruits m^{-2}	leaves/m^2	**0.723**	124
	Fruits/leaves	distance	**-0.465**	124
	Dried fruit mass/dried leaf mass	distance	**-0.190**	124
Strawberry	Leaves m^{-2}	distance	0.045	94
	Flowers m^{-2}	distance	**-0.507**	94
	Flowers m^{-2}	leaves/m^2	**0.753**	94
	Flowers/leaves	distance	**-0.699**	94

Table 1.3. Log-log correlations between soil variables from resin bag and aerobic incubation (inc.) analyses and plant responses along transects from 0 to 15 m distance from the piles. Significant ($p<0.05$) values are bolded.

		NH_4-N (resin) (mg kg^{-1})	NO_3-N (resin) (mg kg^{-1})	Sum major base cations (resin) (mg g^{-1})	P (resin) (mg kg^{-1})	NH_4 (inc.) (mg kg^{-1})	NO_3 (inc.) (mg kg^{-1})	SON (inc.) (mg g^{-1})
Strawberry (N=27)	Leaves m^{-2}	0.060	0.111	-0.062	-0.148	-0.003	**0.409**	0.139
	Flowers m^{-2}	0.159	0.270	0.022	0.157	-0.151	**0.536**	**0.502**
	Flowers/leaves	0.186	0.304	0.122	**0.468**	-0.247	**0.392**	**0.663**
Raspberry (N=28)	Leaves m^{-2}	**0.487**	**0.541**	**0.461**	0.317	-0.004	**0.377**	0.229
	Flowers m^{-2}	0.353	**0.600**	**0.380**	**0.439**	-0.213	**0.505**	**0.681**
	Flowers/leaves	0.186	**0.506**	0.243	**0.423**	-0.261	**0.379**	**0.478**
	Fruits m^{-2}	**0.469**	**0.520**	0.217	0.107	-0.261	**0.379**	**0.478**
	Fruits/leaves	0.349	0.322	-0.045	-0.132	-0.258	**0.333**	**0.491**
	(Flowers+fruits) m^{-2}	**0.448**	**0.577**	0.297	0.250	-0.288	**0.451**	**0.552**
	Leaf mass	0.282	**0.488**	0.249	0.238	0.083	0.192	0.112
	Fruit mass	0.188	**0.533**	0.240	0.246	0.232	0.136	0.014
	Fruit mass/leaf mass	-0.292	-0.281	-0.254	-0.198	0.015	0.239	**0.507**
Cherry (RaR) (resin N=33; inc. N=37)	Individual basal area (cm^2)	-0.207	-0.104	-0.268	0.172	**0.358**	0.280	**0.404**
	Flowers per tree	-0.061	**0.346**	0062	0.158	0.111	**0.345**	**0.450**
	Flowers / basal area	**0.351**	**0.366**	0.121	-0.185	-0.134	0.300	**0.337**

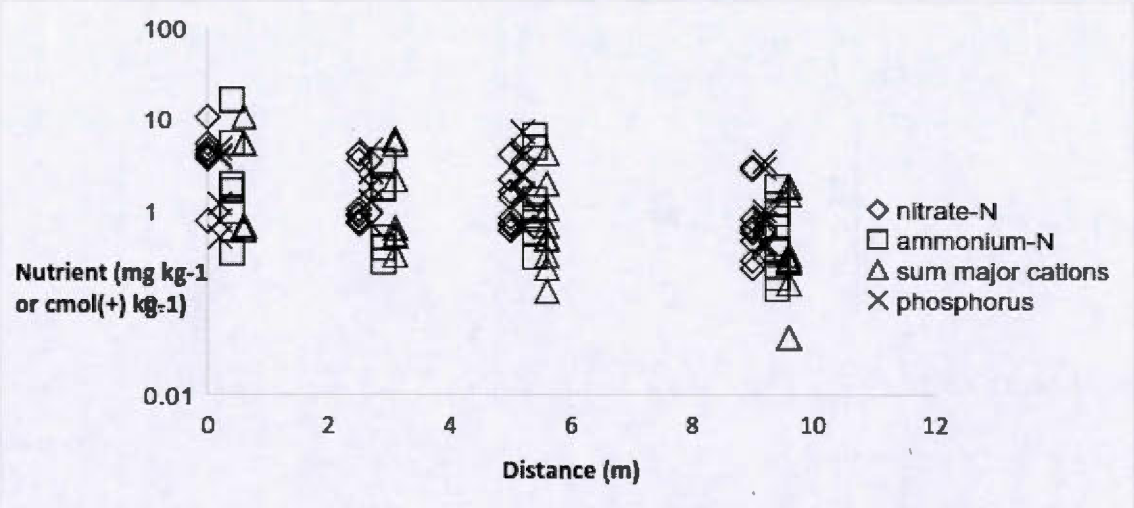


Figure 1.1. Nutrients as a function of distance from piles for resin bag analysis at Riviere-aux-Rats. Distances have been offset from the true distances by as much as 0.6 m to permit the data series to be distinguished from one another.

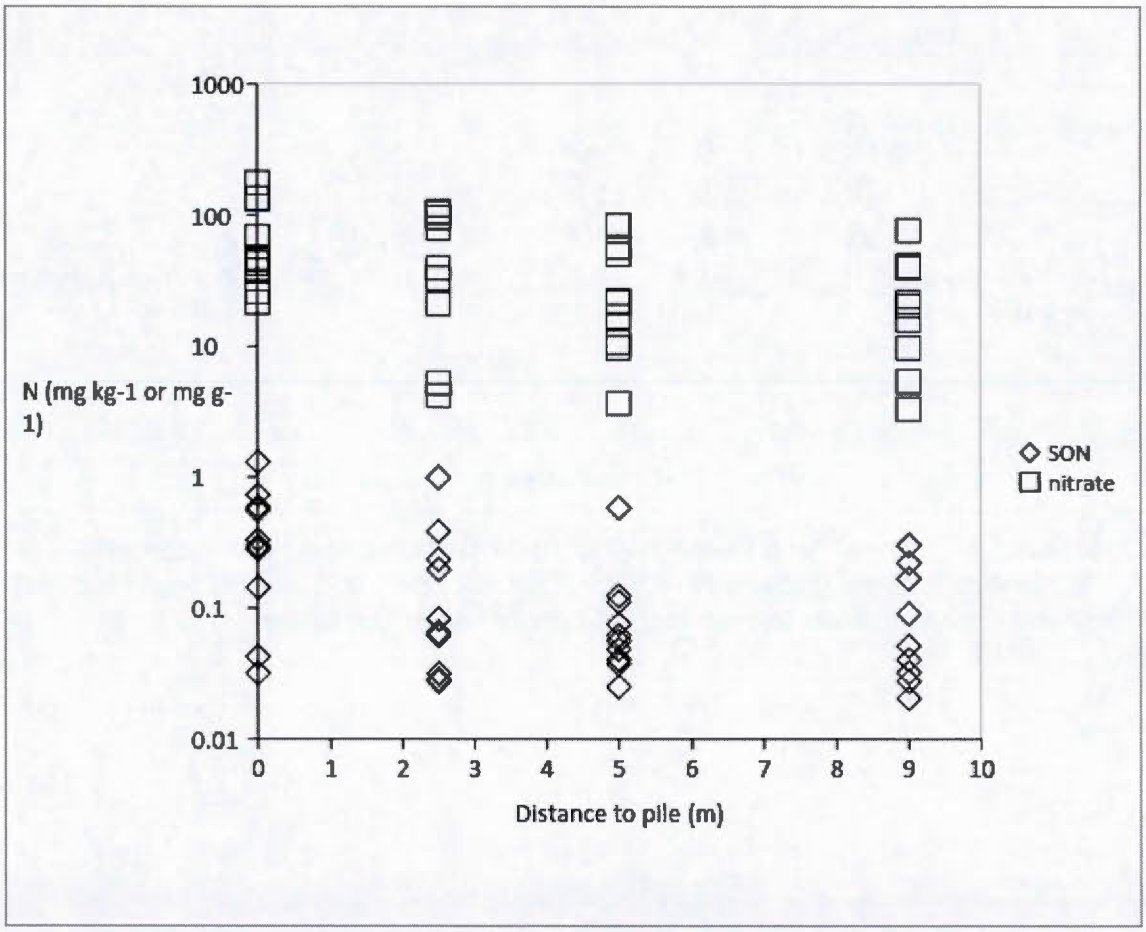


Figure 1.2. Aerobic N incubation results: soluble organic N (SON, mg g^{-1}) or NO$_3$ (mg kg^{-1}) vs. distance (m) to pile.

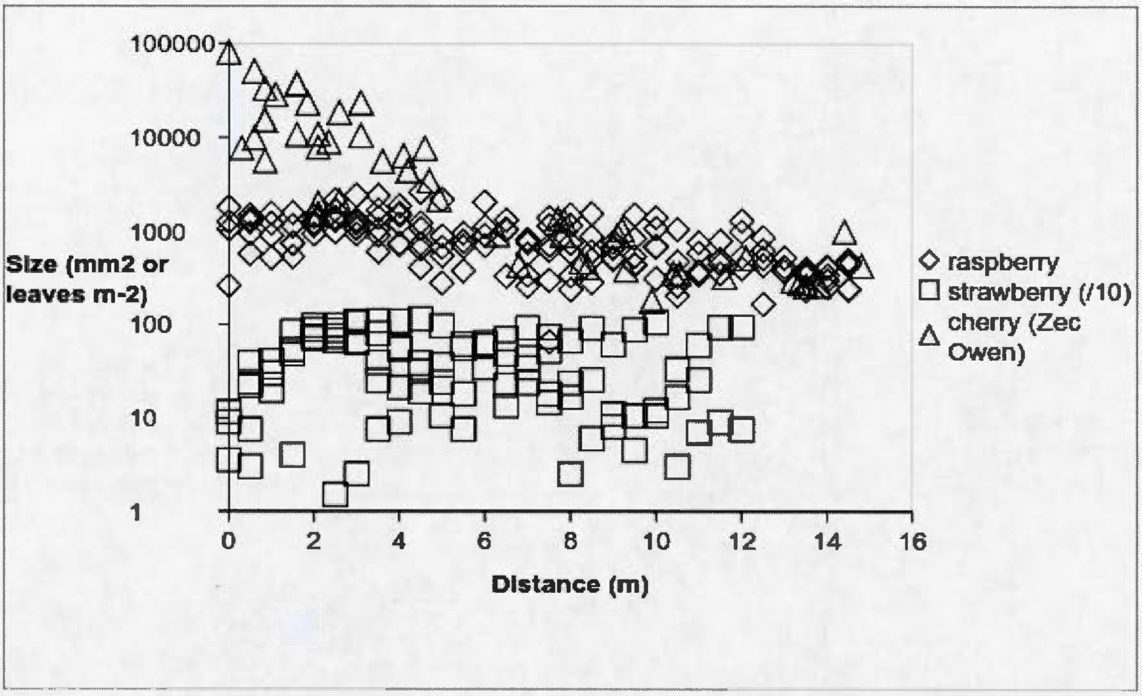


Figure 1.3. Size measures for raspberry and strawberry (leaves m^{-2}) and for cherry at Zec Owen (basal area, mm^2) vs. distance from piles. Strawberry leaf density is reduced by 10-fold for clarity. For cherry and raspberry, the pile edge is at about 2.5 m.

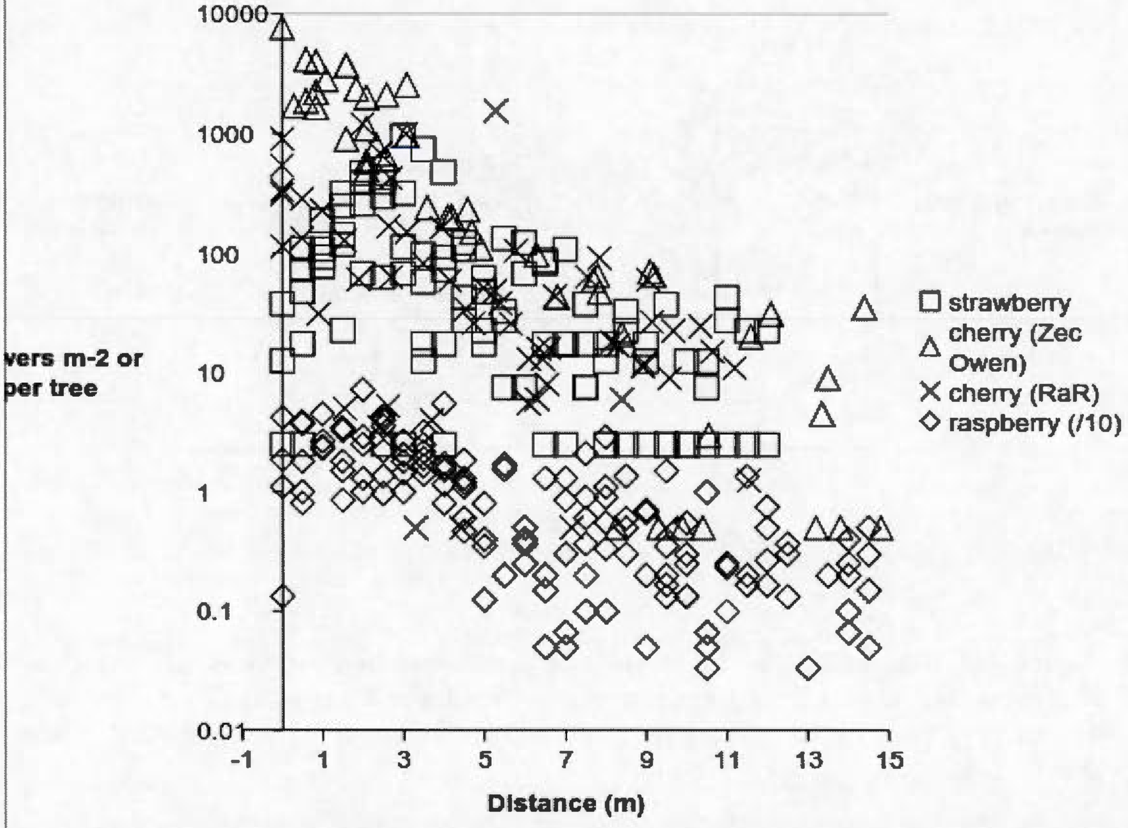


Figure 1.4. Flower production per square meter (raspberry and strawberry) or per tree (cherry) vs. distance (m). Raspberry flower density is reduced by 10-fold for clarity. For raspberry and for cherry at Zec Owen, the pile edge is at about 2.5 m.

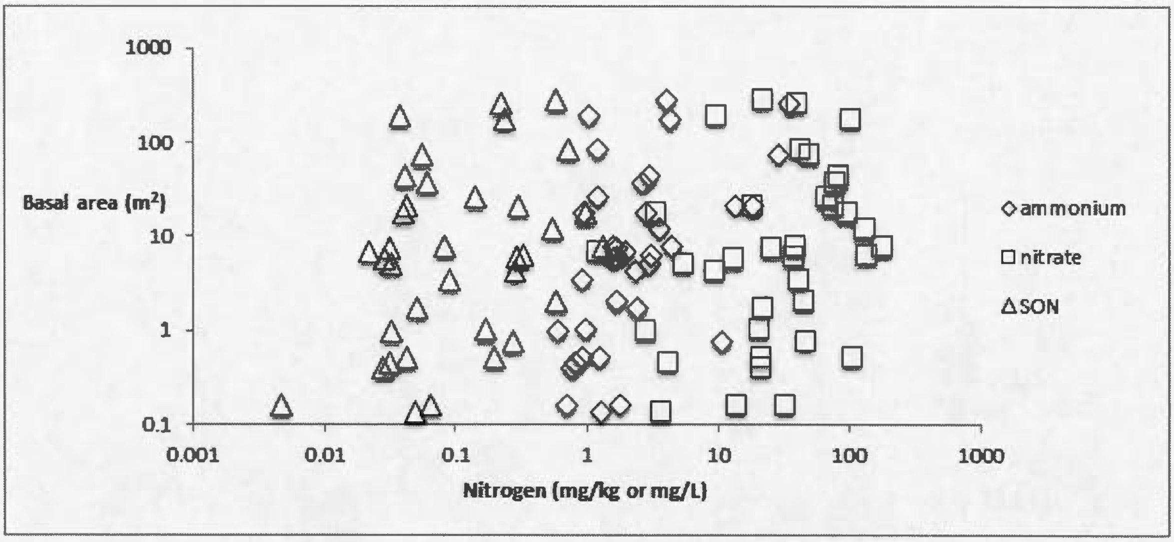


Figure 1.5. Incubation results for soluble organic N (SON, mg g^{-1}) NO_3, or NH_4 (mg kg^{-1}) vs. basal area for cherry at Riviere-aux-Rats.

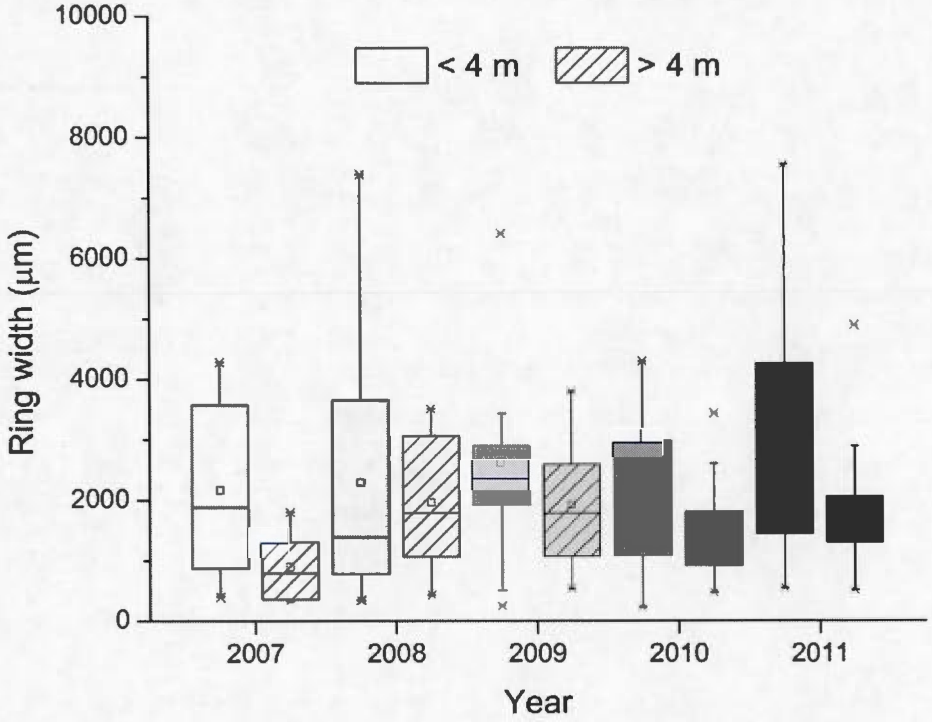


Figure 1.6. Annual relative growth rate of cherry basal area at Riviere-aux-Rats as a function of distance to the pile during the most recent 4 yr. Asterisks denote extreme values.

CHAPITRE II

THE EFFECT OF PROXIMITY TO AGGREGATED SLASH ON THE GROWTH OF HYBRID POPLARS

2.1 Abstract

Forest harvest residue (FHR) may be utilized as an alternative energy source. A hidden cost however, will be lengthened rotation time if trees grow more slowly due to reduced nutrient input. Our objectives were to (i) examine soil nutrition, tree growth, and foliar nutrient status of hybrid poplar (*Populus maximowiczii x P. balsamifera*) as a function of proximity to slash pile; and (ii) estimate the block-scale poplar yield loss at the end of year 6 if all FHR were removed. Using a 6-year-old poplar plantation on sandy loam in Quebec, we found that poplar relative growth rate was faster near than far from piles, and semi-log correlations of tree volume, and soil and foliar nutrients, on distance from pile were significant and inverse, with little effect >12 m. The accrual of wood biomass via propinquity to a pile more than compensated for loss in planting space. We estimate a block-wide volume reduction of 8% by the 6th year if piles had been removed in year 1. Given that the anticipated rotation for hybrid poplar for this site is 20 years, slash retention will lead to either a shortening of the rotation interval or increased yield at the usual time of harvest. The tradeoffs for policy of retaining some or all FHR within the block are discussed.

2.2 Introduction

There is an increasing interest in using post-harvest residue as biofuel (Goerndt et al., 2014; Berger et al., 2013; Stupak et al. 2007). Additionally, the increase of forest fire intensity and total area burned in the last few decades has focused further attention on slash as fuel, and prompted calls for widespread slash reduction in forests (Stephens and Ruth, 2005).

On the other hand, there are positive consequences when harvest residue remains on site. In addition to the benefits for small mammals such as voles (Vanderwel et al., 2010; Rittenhouse, in prep), amphibians (LeGros et al., 2014; Rittenhouse, et al. 2008), and fruiting plant resources for pollinators and frugivores (McCavour et al, 2014; Rost et al, 2012), slash retention has been positively associated with soil nutrient status. Whole-tree harvesting results in a far greater loss of nutrients than would occur if residue were retained on site (Pare et al 2002; Thiffault et al, 2012). More recently, McCavour et al (2014) and Harrington et al (2013) saw an increase in plant growth and soil fertility under higher loadings of slash, and D'Amato et al (2012) saw a reduction in fertility on sandy sites by year 20 when slash was removed. Because of these concerns, biomass harvesting guidelines have been developed with the goal of preventing long term productivity loss as well as limiting harm to the many species that benefit from slash (Herrick et al, 2009; Evans et al, 2013).

The spatial distribution of slash has rarely been discussed when considering the effect of harvest residue on soil fertility and plant growth (McCavour et al, 2014). Specifically, where slash is well-aggregated, one would expect greater growth near slash piles than further away. Indeed, the variability in the literature on the subject of soil nutrient effects on growth may be due to the lack of spatial detail typical of such studies. However, any such expectation will be confounded by the fact that there is more light available over the pile as well as lessened competition for the soil nutrients and water beneath it. One way to separate these effects, as will be shown here, is to use the law of constant final yield. That is, we can ask if plants near piles are producing more biomass per area (with area defined to include both the pile and the adjacent ground) than conspecifics far from any piles.

Our primary objective in this paper is to examine soil nutrient status and the growth of young hybrid poplar (*Populus balsamifera* X *P. maximowiczii*) on a sandy site as a function of distance to slash piles. A novel aspect of this study is the use of the law of constant final yield to separate the effects of the relaxed competition above and below piles vs the nutrient augmentation to the soil under and near piles. We focus on young poplars on sand because nutrient effects should be easiest to discern (Janowiak and Webster 2010); their low nutrient status should make any additional N or P near piles a salient observable resource. Further, this hybrid has been shown previously to be sensitive to site fertility status (Bilodeau-Gauthier et al., 2009; Truax et al., 2012). Additionally, we focus on a young stand to ensure that canopy closure has not yet occurred, thus eliminating potential growth differences that may arise as some trees become tall enough to shade competitors. Finally, a merit of studying these hybrids is that the planted stems are clonal and thus any growth differences must have an environmental cause.

2.3 Methods

To evaluate soil fertility and poplar growth as a function of distance to pile, we used a 6-year-old hybrid poplar plantation on sandy soil at Riviere–aux-Rats, in the Goulet sector of the Haute Mauricie region of Quebec (N 47.292; W 73.038). The site is characterized by type 1 sandy till soil of moderate drainage; a humo-ferric podsol. The pre-harvest canopy was a mix of white and black spruce (*Picea glauca* and *P. mariana*), balsam fir (*Abies balsamea*), balsam poplar (*Populus balsamifera*) and yellow and paper birch (*Betula alleghaniensis* and *B. papyrifera*).

The site was whole-tree harvested with de-branching at the roadside, and then site-prepared with 1 m mounding in 2005. Poplars were planted at a spacing of about 2x2 m in 2006. Asexual regrowth of competing woody stems (mainly pin cherry, *Prunus pensylvanica*) was treated via brush sawing in 2007-2008. The sawing was as intense near as far as from piles; all cherries, irrespective of distance from a pile, had sprouts arising from a sawn base.

The slash piles at this site were found in two sets of 6, the sets separated by about 300 m. Within each set, the piles were about 20 m apart, and did not vary much in size: 200 to 500 m^3 (including air space). The piles in one set were arrayed as a row along a gentle slope at right angles to the contours, and the piles in the other set were in a row along the contours on the footslope.

In 2012 at both sets of piles we sampled every poplar within 25 m of any pile, measuring diameter just above the root collar. In analyses we used the formula of Truax et al. (2014) for hybrid poplar in southern Quebec to relate diameter (cm) to stem volume (dm^3). Survivorship was high, with only a very few of the poplar stems stunted, with missing terminal shoots, or chlorotic leaves. We removed from the analysis any stem with a diameter <4.2 cm as this small percentage of the stems invariably showed heavy browsing at an early age (terminal bud loss). Likewise, a few stems larger than this were bent sideways and these too were ignored. In sum, about 5% of all sampled poplars were not included in the analysis, leaving N=1511.

For the 9 of 12 piles for which we had resin data, we evaluated soil fertility using 2 to (more typically) 3 transects radiating out from each pile edge (a total of 25 transects), with distances to pile of 0, 2.5, 5, 9, 14 and 20 m. When the 14 and 20 m distances were within 12 m of another pile, those data were not used (to avoid multiple distance effects).

The soil fertility methods and results were reported in detail in McCavour et al. (2014). Here we only highlight the main methods. In late August 2011 a total of 190 resin bags (39 at 0m; 40 at 2.5 m; 35 at 5 m; 27 at 9 m; 26 at 14m; and 23 at 20 m) were placed in the soil along the transects, and left *in situ* for approximately 10 weeks and recovered in early October 2011.

In mid-August of 2011, poplar foliar samples (N=170) were collected from trees at the set of 6 piles arrayed across the contours, within 2 m on either side of the resin bag transects. Ten leaves were collected from the topmost sun leaves of the canopies. The foliar samples were placed in small paper bags, immediately transported to the laboratory (CFS, Quebec, QC), dried in an incubator at 55 degrees C for 72 hours, and their dry mass measured.(averaged for each set of ten leaves) Carbon and nitrogen were analyzed on a Leco CNS-2000. A subsample was washed at 500°C and the ash recovered in HCl 1M (Kalra, 1998). Phosphorus and base cation concentrations were determined by ICP (Perkin Elmer Optima 7300DV).

To examine the early growth response of the poplars near (<6 m) and far (>12 m) from piles, we selected in the late summer of 2011 the 5 tallest poplars for each distance category that were within 2 m of one of the resin bag transects. We cut a disk near the root collar for each tree, sanded it in the laboratory, and measured ring widths under the microscope using three different radii from the pith to the most recent ring. Subsequently, we used the mean ring width from the three radii.

2.3.1 Statistical Analysis

T-tests of log values of soil or leaf attributes or poplar size indicated no significant differences (p ranging as 0.13 to 0.78) between the two sets of piles despite the fact that one set of piles was along contours and one set perpendicular to the contours.

Likewise, within the latter array, perpendicular to the contours, ANOVA showed no discernable effect of the piles (p ranging as 0.24 to 0.86). We also found no differences due to transect direction (north vs south; east vs west) using t-tests of log-transformed values (p ranging as 0.21 to 0.90). Subsequently therefore, data from the two pile arrays and transects were combined, and in all subsequent statistical treatments we used Pearson product moment correlations of the transect-averaged values because we no longer had reason to explicitly treat the effect of an individual site or pile. As with McCavour et al (2014), we (1) used log-log correlations to relate fertility measures to plant attributes and (2) used semi-logarithmic correlation for any distance effects because the curvilinear data in the regressions could best be represented by a log-transformation of the plant attribute as a function of distance to pile. However, when we turned to partial correlations to tease out the inter-correlated effect of the two abiotic measures on an attribute, we used log-log. Finally, because there was a tendency for both soil and poplar diameter to asymptotically flatten at distances of about 8 to 15 m from a pile edge (as with McCavour et al., 2014), all regressions were based solely on the subset of data at distances of 12 m or less from a pile edge.

2.3.2 Modelling the contribution of near-pile trees to total standing volume

If resources such as light, water, and soil nutrients are more or less homogenously distributed across the harvest block, then the law of constant yield (Weiner and Freckleton, 2010) argues that individual trees at locally low density (e.g. near the edge of a pile) may well grow faster than elsewhere, as they have more resources to exploit, but their total biomass *per area* (pile area included) cannot exceed that of the more dense areas. More formally, and envisioning for simplicity a slash pile as a circle, at distance x away from a pile edge the tree volume per area, V_{x+r} would be:

$$V_{x+r} = \sum V_x / \pi\,(x+r)^2 \qquad (1)$$

where $\sum V_x$ is the sum of the volume of all trees from the pile edge to x, and r, the pile radius, averaged 5.57 m for our 12 piles. Note that although the trees near the edge might be larger than elsewhere, the local density measurement takes this into account by including the pile, an area *where no trees were planted.* Letting V_c denote the volume per area beyond x, the constant yield argument then becomes:

$$V_c \geq V_{x+r} \qquad (2)$$

If following the law of constant yield, the inequality in (2) may be large until canopy closure, because light receipt would not initially be reduced while all the trees were small, while poplar density near the piles remains small because of the inclusion of pile area in the calculation of volume/area. Subsequently, as adjacent crowns began to touch, trees near piles would receive more light than those farther away. With the Law of Constant Yield, assuming equal soil nutrition, one can have many smaller trees, or fewer larger trees, but the overall biomass will be the same (the reader likely remembers the experiment as an undergraduate dry-weighing carrots-the 10 [large] carrots in their 4*4 growing tray had the same dry weight-biomass- as the 30 [small] carrots in their other 4*4 growing tray. So, with our poplars, we have fewer, larger trees in blocks that contain slash piles (the piles themselves are not planted and so represent lost planting space) and more numerous smaller trees in blocks where there are no piles. The law permits trees near edges of piles to be larger than elsewhere, but their volume *per area* (pile area included) cannot be larger than the volume per area in the rest of the block (where there are no slash piles, and therefore more [smaller] trees).

2.4 Results

2.4.1 Tree size as a function of distance from pile

There was a sharp decline in poplar volume (dm^3) with distance up to about 12 m; beyond which there was little change (Figure 2.1). Restricting the correlation therefore to the 848 poplars that were <12 m from a pile, the semi-log correlation was significant ($r=-0.415$; $p<0.0001$). While small trees can be found anywhere in the block, large trees were essentially limited to the area near the piles (Figure 2.1). Indeed, of the 105 trees with a size greater than 40 dm^3 and with a distance from pile of between 0 to 25 m, only two of these trees were found more than 8 m from a pile. On average, the trees within 4 m of a pile (N=309) had a mean volume 2.4 times greater than those from 4 to 25 m away (N=1202).

2.4.2 Foliar analysis

For the 133 poplars (within 12 m of a pile) used for the foliar analysis (Table 2.1), log-log correlations of leaf attributes with distance from pile showed significant correlations for all but dry mass, magnesium and zinc concentrations (Table 2.2; Figure 2.2). Tree volume (dm^3) had significant correlations with all variables except sulphur, phosphorus, calcium, and magnesium (Table 2.2).

Given the dependence of tree size on distance to pile, partial correlations were used to separate distance and foliar contributions for those size correlates that were significant. Distance had stronger partial correlations than tree size only for potassium and iron (Table 2.2). In particular, tree size (rather than distance) had much stronger partial correlations for leaf mass, nitrogen and carbon.

2.4.3 Soil analysis

McCavour et al. (2104), in their analysis of soil fertility, growth and flowering among fruiting plant species, discussed in detail the results of the resin bag analysis and soil incubation analysis as a function of distance to pile. (See Chapter 1 or McCavour et al. (2014): Figures 1.1, 1.2; Table 1.1) Here we focus on the fertility results in relation to poplar volume. For the nine piles for which there are resin data (at distance category mid-points of 0.5, 2.5, 5, and 9 m), and limiting the semi-log correlations, as above, to distances <12 m from a pile, the correlations with distance for NH_4-4, NO_3-N, sum of base cations, and phosphorus were negative with distance from pile (high near piles) and, except for P, significant (with correlation coefficients of -0.439, -0.61, -0.421, and -0.313, respectively; N=33; Table 2.2).

Averaging across the same four distance classes for poplars for distances <12 m (N=338), the semi-log correlation of size with distance was -0.655. In turn, the semi-log correlations between tree size and each of the four soil measures (N=33) were positive, and were significant for NO_3-N (r=0.580) and the sum of base cations (r=0.405).

A partial correlation analysis using this same subset of trees showed that soil nutrient status and distance were about equally predictive of tree size. With tree size held constant, all the partial correlations of nutrient concentration with distance were inverse and, except for NH_4-N, significant ($p<0.05$; N=33). Similarly, with distance held constant, three of the correlations with diameter (but not the sum of base cations) were significant ($p<0.05$).

2.4.4 Growth rates and distance to pile

Two years following planting (end of 2006) the trees were of equal size (Figure 2.3). Despite the small sample size (N=5 largest stems for each distance type), the trees in the two distance categories were statistically different by 2011 (t-test of log values; p=0.033). (In 2010, p=0.053.) Qualitatively, the divergence in growth rates can be discerned by 2009 (two years after planting; Figure 2.3), with the growth differential between poplars growing near piles and far from piles accelerating with time.

2.4.5 The effect of pile-enhanced growth on yield at the scale of a harvest block

At seven years of age (six years after transplanting into the block), the area of the large piles, as defined by the perimeter, comprised in total 1.7% of the total harvested area (excluding the area contributed by a few very small piles or shallow patches of logging residue found near landings). Far from any pile, for example where $x>16$ m, the average size of a poplar was 9.39 dm^3 while the volume/area (V_c in equation 2) was 2.35 dm^3/m^2 (Figure 2.1). This would be the block-wide yield at this age if there were no piles. By contrast, within a distance of 4 m from a pile where the soil nutrient effects of slash are greatest, the mean volume was 27.5 dm^3 and, including the unplanted area of the piles, the mean polar volume per area (V_{x+r} in equation (1)) was 6.34 dm^3/m^2. Clearly, we are violating the assumptions in equation (2) underlying the law of constant yield. That is, the additional growth seen near piles cannot be due merely to extra resources available at a low, local density; there must be additional resources near piles (such as additional soil nutrient supply) in an amount that is *at least* 2.7 (=6.34/2.35) times greater than elsewhere in the block.

2.5 Discussion

As McCavour et al. (2014) found at this same site for three fruiting, non-commercial plant species, there was an exponential decline in volume with distance from pile out to approximately 12 m. All but two of the 105 poplars with a volume exceeding 40 dm^3 were within 8 m of a pile. These trees were so much bigger than others that a very large fraction of the woody biomass in the block was in the small area adjacent to piles. Not surprisingly, the trees near the piles tended to have high mineral content in their leaves (especially K), and soil nutrients, especially nitrogen, declined exponentially with distance to about 12 m. Finally, we showed with analysis of the annual basal increments that this growth advantage for the biggest near-pile stems, relative to the biggest stems much further away, began within about three years after planting.

What could cause this growth enhancement near piles? It cannot be exclusively the extra light above the pile because the trees have not yet achieved canopy closure; near-pile stems might have additional sunlight only in the morning or late afternoon. Further, it is likely that lessened competition for water and below-pile nutrients made a contribution to this differential growth.

However, as we saw with the constant yield analysis, any augmentation from resources above or below the pile based solely on reduced competition (low local tree density) is insufficient to explain the much greater mean poplar size near piles. That is, there must be an *additional* source of resources near piles, and the results from the soil resin and foliar analyses show that this additional source is nutrient supply, especially nitrogen, from the pile as it decomposes.

Presumably, the initial growth advantage of what would become the large trees near piles was due to the rapid decomposition of the fine woody debris (mixed in with larger pieces) at the base of the pile. Hybrid poplars are fast-growing plants, and as seen here, and as conceptualized by Grime (1979), have a concomitant high capacity to acquire nutrients and alter their uptake in response to growth at varying nutrient levels. These characteristics that allow the poplars to compete effectively with their neighbors by reducing external concentrations of resources to unusably low levels (Tilman, 1988) and reducing leakage of nutrients out of the root in poor soil (Kronzucker et al., 1997) likely increase their ability to utilize the extra resources from slash piles relative to planted stock such as pine or spruce. Messier et al. (2009) postulated that the spectacular growth of hybrid poplars sometimes observed may be in response to a low competition below ground environment; a response partly due to the natural selection for root avoidance or segregation by early-successional tree species as a strategy to optimise uptake of below-ground resources for fast, aggressive early growth.

Additionally, hybrid poplars preferentially take up NO_3, a more available source of N in the typically higher pH soil present post-harvest than the NH_4 preferred by many of the native plants adapted to poor soils (Kronzucker et al., 1997). McCavour et al. (2014) saw a similar skew in growth advantage near piles for pin cherry, an NH_4-philous species, and a concomitant strong partial correlation with soil NH_4-N and other fertility measures.

One presumes that with time, somewhat larger pieces of fine woody debris at the pile base would sequentially add to the resource, and coarse woody debris within the pile base, though possessing a less favourable C:N ratio than fine wood, would likely be contributing to the high level of soil fertility observed near piles after only a few years. We expect that the growth advantage shown here for near-pile poplars will continue for at least several more years, as other piles at older plantations (17 years) are only now at decomposition stages approaching ground level.

We have found only one other study that clearly relates the growth of planted stock to distance from aggregated slash, though in a somewhat different way than in our study. Ballard (1978) compared the growth of evenly-spaced 7-year-old *Pinus radiata* on a sandy site in New Zealand. The parallel windrows were about 9 m wide and quite shallow, occupying about 30% of the site, with inter-windrow areas about 20 m wide. The growth of pines planted *on* the windrows (our piles were not planted) was compared with those planted in the inter-windrow spaces. He found that pines on the former averaged about 2 times greater volume/area than those on the latter. Recall that we found that poplars within 4 m of a pile were 2.7 times larger than those much farther away (when including, as with the *P. radiata*), the area of the pile). While one might hypothesize that the effect of windrows on the pines' growth might be mainly due to its role as a mulch in the more arid climate where Ballard (1978) worked, the similarity of the differential volume growth between areas with slash or no slash makes it likely that the result was due, as we argued here, primarily to nutrient augmentation. Further, while Kronzucker et al (1997) and many others have published evidence of poor utilization of NO_3 by conifers, more recently Bown et al (2010) questioned the purported preference for NH_4 over NO_3 by *P. radiata* and found that although N uptake was higher on NH_4 dominated soil, N use efficiency was lower (partly due to lower rates of light saturated photosynthesis than when grown in high NO3 soil), resulting in better seedling growth on NO_3-dominated soil, such as on disturbed sandy sites such as our and Ballard's post-harvest sites.

We caution that this conclusion regarding the effect of nutrient leakage from piles on tree growth may be species- and site-specific; data from combinations of soil type and tree nutrient requirement is needed to assess the effects on other species. We deliberately chose a combination of low fertility (a sandy site) and a very nutrient-demanding tree species with potentially fast growth in the hope of discerning a clear effect of nutrient augmentation from the piles. A species more tolerant of low fertility or a site with a better nutrient status would have undoubtedly provided a less dramatic growth response to proximity to a pile.

The enhanced growth near piles means that the block could be harvested earlier than planned, rather than simply harvesting the higher than expected biomass at the planned rotation time of about 20 years. (A third alternative, having a separate rotation interval for trees near vs far from piles, is unwise as the area near piles is only a small percentage of a harvest block.) While we have every reason to assume from Figure 3 that the divergence in size between the trees near vs far from piles will only increase with time, nonetheless we can pretend that the trend will not continue, and estimate the reduction in rotation time assuming that the trees only maintain their seventh-year relative size difference. Comparing volume per area for trees within 4 m of a pile (again, including the unplanted pile area) with trees found much farther away, the rotation time could be reduced by a minimum of 8% because the pile area plus the area 4 m away now comprises not 1.7% of the area (piles alone) but 5%.

Further, given that much of the early decomposition of the post-harvest residue must be at the pile base, if slash was left as numerous smaller piles, there could be an additive effect on the shortening of the rotation. Well-distributed piles with half their present volume (but the same individual area) at this site would then, along with the adjacent area <4 m away, comprise 10% of the block, reducing the rotation time by 15%. This additive process would soon however reach an asymptote as we approach the point where piles become so sparse that their augmentation of soil nutrients is less than what was observed at our site.

In short, rotations could be lessened if piles were retained at a nutrient-poor site, and especially if more numerous and shallow piles were preserved. It is beyond the scope of this paper to calculate the trade-offs between the economic value of removing post-harvest residue for biofuel or fire hazard reduction so that it can be compared with the value of reduced rotation time, as these trade-offs depend strongly on soil type, transportation costs and ecological requirements, but at the very least this result should caution us from assuming that removal is necessarily the best economic solution within the context of managing forests for optimal output.

Additionally, this result is of particular interest to those who wish, or are mandated, to practice sustainable forest management. Achieving higher yields from smaller portions of the forest landscape means that more forest can be set aside as conservation or low use (as demonstrated in the TRIAD experiment in Quebec; Messier et al., 2009). Further, as shown by McCavour et al. (2014), the population sizes of many of the non-commercial plant species greatly benefit from the relaxed competition with the planted species that exists initially near or on piles. These species produce far more biomass, flowers and fruits in the presence of piles, and with time begin to colonize the surfaces of the piles themselves. The area (but not the volume) of the pile is crucial for these species because as canopy closure of the plantation ensues elsewhere, these piles remain clement sites for light-demanding herbaceous and small woody species such as strawberry (*Fragaria virginiana* Mill) or raspberry (*Ribes ideaus* L.) to at least the end of a short rotation.

Thus increasing the pile number by reducing individual pile volume (but not area) will simultaneously lead to lower rotation times as well as satisfy the demands of flowering plants and, in turn, the pollinators and frugivores dependent upon them. Piles contribute then to the maintenance of landscape connectivity for species that respond positively to their presence, and in some jurisdictions, may allow forest managers to attain greater yield and sustainable forest management credit or certification.

That is, we perceive slash as a management tool to achieve a large number of ecological goals (biodiversity, ecosystem services) as well as more strictly economic ends (biofuel, fuel reduction, shortened rotations on nutrient poor sites). The actual decisions made by managers will of course depend on economic markets, local energy sources, and local or regional concerns such as protection of important or endangered forest biota or services.

2.6 Tables and figures

Table 2.1. Mean values from poplar foliar analysis. The first three columns are a percentage, while the remainder are g kg^{-1}.

C	N	S	P	K	Ca	Mg	Mn	Zn	Al	Fe
1.81	1.53	0.22	3.00	14.26	7.47	2.45	0.66	0.30	0.05	0.03

Table 2.2. Log-log correlations of foliar and soil nutrients with distance from pile (0-12m). Significant ($p<0.05$) results are bolded. Also shown are the log-log partial correlations with distance to pile and diameter (dm^3) for those quantities where tree size alone had yielded significant correlations.

Correlate	Partial correlation with distance to pile	Partial correlation with volume (dm^3)	Correlation with distance to pile	Correlation with volume (dm^3)
Foliar				
Dry mass	0.069	**0.506**	-0.183	**0.526**
C	**-0.110**	**0.332**	**-0.269**	**0.410**
N	-0.072	**0.538**	**-0.315**	**0.595**
S			**-0.270**	0.023
P			**-0.210**	0.034
K	**-0.505**	0.101	**-0.571**	**0.327**
Ca			**-0.196**	0.177
Mg			**0.398**	-0.170
Mn	-0.183	**0.432**	-0.029	**0.397**
Zn	0.136	**-0.330**	0.016	**-0.301**
Al	**0.196**	**-0.307**	**-0.341**	**-0.409**
Fe	**-0.296**	**0.256**	**-0.417**	**0.392**
Soil				
NH_4-N	-0.16	**-0.369**	**-0.439**	**0.227**
NO_3-N	**-0.804**	**-0.486**	**-0.61**	**0.580**
Sum of base cations	**-0.557**	-0.299	**-0.421**	**0.404**
P	**-0.411**	**-0.331**	0.313	**0.036**
Poplar size			**-0.655**	

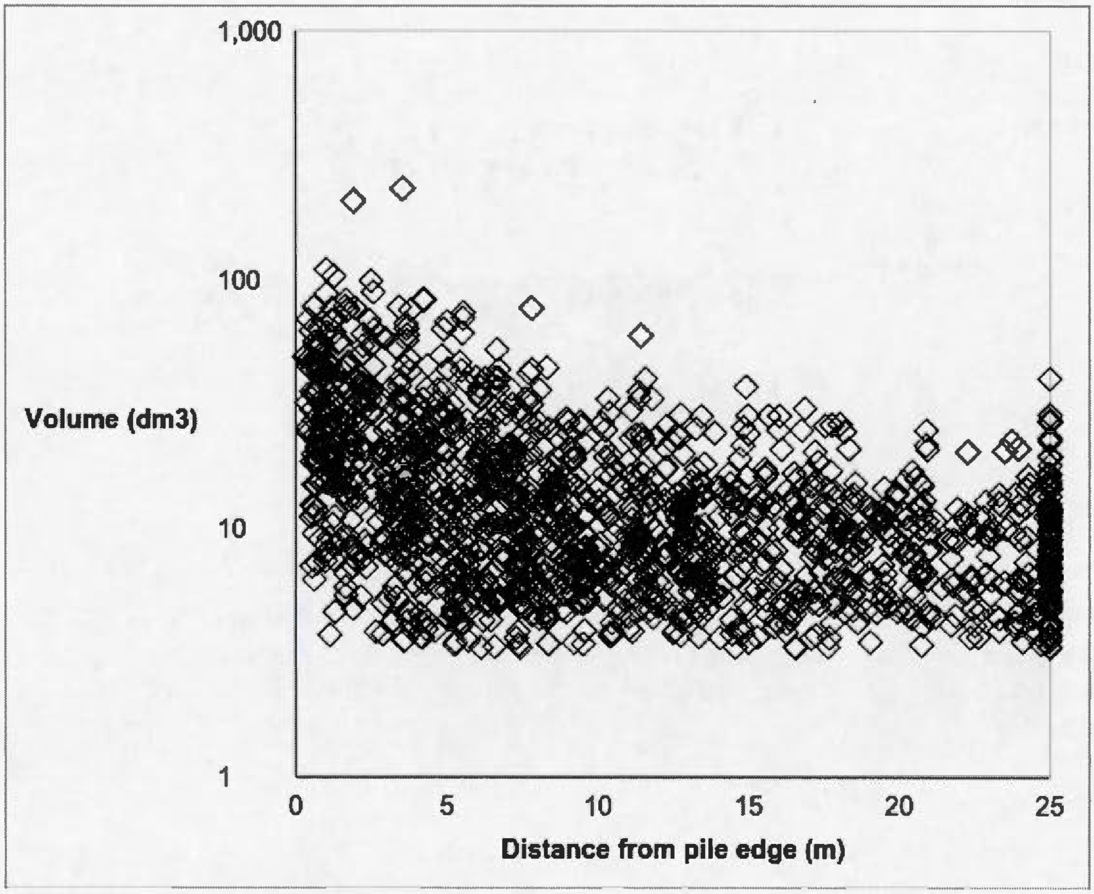


Figure 2.1. Tree size (dm^3) as a function of distance from pile (m). N=151.

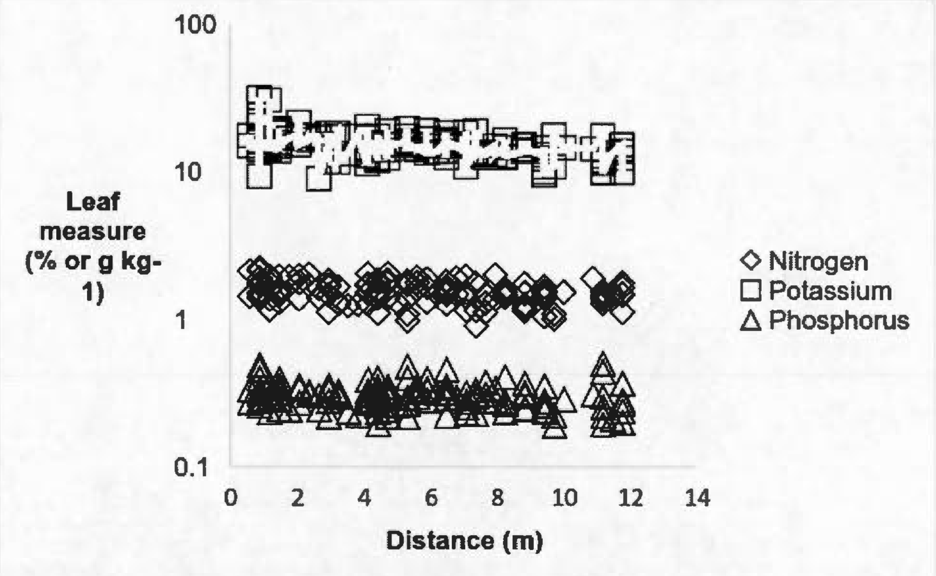


Figure 2.2. Examples of the decline in leaf measures with distance from pile for the foliar analysis. Nitrogen is given as a percentage of dried mass while phosphorus and potassium are in g kg^{-1} of dried mass. Phosphorus is reduced by 10 times for clarity.

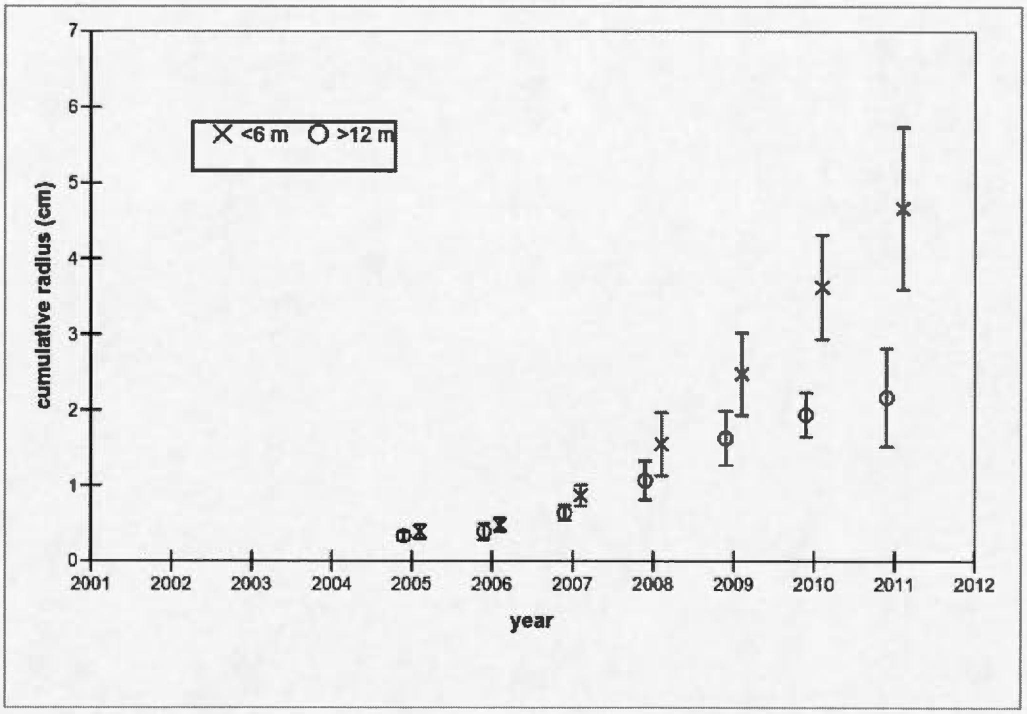


Figure 2.3. Cumulative ring width with sample standard deviations for trees near and far from piles.

CHAPITRE III

FOREST HARVEST RESIDUE LOADING AND THE JUVENILE SURVIVORSHIP OF SMALL-SEEDED TREE SPECIES

3.1 Abstract

The role of slash depth in relation to germination and establishment of forest plants in clearcuts remains unknown, despite the desirability to managers of being able to predict and select for parameters favourable to natural regeneration, or maintenance of abundance and/or diversity of species. We hypothesized that juvenile survivorship would (1) initially rise with slash loading because partial shade would reduce evapotransporative loss but then (2) begin to decline at greater loadings due to seed trapping in bark crevices as well as increasing shade. In a one-month old clearcut on sandy loam we collected and used size-classed slash from a large pile to create 1x1 m slash aggregations varying in loading from 0 to 60 kg/m^2. In each aggregation we sowed seeds of yellow birch and white spruce, both small seeded species. The two species showed a similar response, with a maximum survivorship occurring at 4 (birch) or 8 (spruce) kg/m^2. The optimal range for seedling establishments was for loadings between 2-12 kg/m^2, which is quite similar to the range of mean block-wide values reported for cut-to-length operations.

3.2 Introduction

The removal of slash for bioenergy or for fuel reduction in co-generational mills has been increasingly important (Parzei et al., 2014); not surprisingly, this has prompted a renewed interest in the potential benefits of slash for plant regeneration and growth. While recent studies have examined the beneficial effects of slash on soil fertility and plant growth (Thiffault et al., 2011), as well as on many bryophytes and flowering understory species (Astrom et al., 2005; McCavour et al., 2014), the effect on post-harvest sexual recruitment has remained unclear.

Studies of the role of slash removal in plant sexual reproductive success using paired blocks that were whole-tree harvested (majority of slash removed) versus cut-to-length (moderate slash remaining) have tended to show better post-harvest recruitment from seed where slash removal is greater (Mann, 1984; Scherer et al., 2000). These authors attribute their results to the greater disruption of the fibric organic layer however (as entire trees are skidded) rather than to wood removal.

On the other hand, for small-seeded species, adequate moisture availability is the main arbiter of juvenile success. Indeed, this is why duff disruption is so influential; it permits the radicle to reach the mineral soil or the high bulk density humus layer (Greene et al., 1999). Slash reduces evaporative water loss from the mineral soil surface (Lieffers and Van Rees, 2002; Olsson and Staaf, 1995; Bråkenhielm and Liu, 1998) and thus increases juvenile survivorship (Smith, 1951; Alexander, 1987). Finally, shading and increased moisture availability combines to greatly reduce the likelihood of lethal surface soil temperatures in the first growing summer after a clearcut (McInnis and Roberts, 1995).

While fresh wood itself is not a viable seedbed (Greene et al., 1999), rain readily washes seeds off cylindrical pieces of wood onto the adjacent substrate, especially given that bark crevices are not yet well developed on the small-diameter stems predominant in slash. Although it has never been quantified, very large slash loadings should however prevent many of the deposited seeds from reaching the ground. That is, layers of woody pieces will undoubtedly trap seeds at the edges of the zones of contact between them.

We hypothesize therefore that juvenile survivorship (the ratio of seedlings to seeds) will, because of improved water availability and lessened mortality from very high temperatures, rise with increasing slash loading up to a mode and then decline due to seed trapping. We will test this hypothesis by sowing seeds on a gradient of small, well-defined slash loadings.

3.3 Methods

In November of 2012 we created 0.5 by 0.5 m slash accumulations in the middle of a one-month-old clearcut that had been whole-tree harvested. The cut was near Riviere–aux-Rats in the Goulet sector of the Haute Mauricie region of Quebec (N 47.292; W 73.038). Total annual precipitation is 93 cm. The site is characterized by a sandy till soil of moderate drainage (humo-ferric podsol). Generally, the substrate at the harvest site consisted of exposed mineral soil and exposed humus, with occasional patches of duff that had not been disrupted by the operation.

The wood was taken from slash piled at the landing and was mainly composed of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*) and paper birch (B. *papyrifera*), and pin cherry (*Prunus pensylvannica*). It was sorted into six diameter classes and was about 60% fine woody debris (<10 cm diameter) by mass. Aside from the few very large pieces (>15 cm diameter), which were not used, we attempted to maintain the same proportional distribution of mass for each loading as in the original pile, using a weigh scale to measure mass. These green weight loadings ranged from 0.2 kg/m^2 (the “control”; i.e. no wood was added) to 60 kg/m^2, thus covering the range of reported values at the scale of a few meters from the literature for slash that has not been deliberately piled. There was a total of 13 different loading values, mainly concentrated in the range 2-12 kg/m^2, as these are the most common values reported (e.g. Alam et al., 2012; Relvic et al. 2007) following cut-to-length harvesting. There were two replications per loading value for a total of 26 plots. All pieces larger than the 0.25 m^2 plot size were trimmed to length with a saw. Pieces were laid in a random set of orientations in the horizontal plane.

The artificial piles were allowed to settle over the winter. In April of 2013 after the snow had melted we sowed 200 filled seeds each of two commercial species, white spruce, and yellow birch. Seeds were obtained from the Ministere Ressources Naturelles du Quebec. The former has a mean mass of 2.3 mg while the latter has a mass of 1.0 mg. The seeds were sprinkled within the central 50% of each plot area. In November of 2013, well after the germination and establishment period of the summer, the piles were carefully taken apart. While the lowest layer of wood was still present, the percent of the plot area with exposed ground was estimated visually. Then the last pieces of wood were removed, and the number of seedlings counted. None of the species was having a mast year in 2012 and thus it is exceedingly unlikely that these plots, 150 m from any standing trees, had recruits from any source other than the sowing.

3.4 Results

Figure 3.1 depicts the survivorship (S=seedlings/seeds) vs. the loading (kg/m^2) as of November of the first growing season. The modal survivorship was at a loading of about 4 (yellow birch) or 8 (white spruce) kg/m^2. There was no significant difference in the distribution of survivorship between replicates for either species (K-S test; $p>0.05$). Between species, however, there was a significant difference; yellow birch seedlings were shifted toward lower loadings than spruce seedlings (K-S test; $p=0.019$).

The proportion of soil covered by woody residue rose linearly with loading until about 2 kg/m^2 at which point it increased asymptotically to 100% (Figure 3.2). There was no exposed ground at loadings greater than 24 kg/m^2.

To understand how the unmeasured trapping of seeds and shading increased with loading it is useful to recalculate survivorship as S/p where p is the proportion of ground covered by wood (Figure 3.3). The peak loading then becomes 12 kg/m^2. Nonetheless, from 12 to 24 kg/m^2, as S/p sharply declined to 0, there was still exposed ground (from 1 to 10%). Clearly, trapping and shading increased with loading from about 4-8 (the modal values for S) to 24 kg/m^2.

The mean S values for loadings less than 28 kg/m^2 were 0.042 or 0.046 for white spruce and yellow birch, respectively. These two values were not statistically different (N=20 for each species; difference of proportions test; $p=0.32$). Using S/p across the same loading range, the survivorship values were 0.24 or 0.18, respectively; again, not statistically different (t-test).

3.5 Discussion

Although the available substrate for germination declined from about 100% to 0 by the 28 kg/m^2 loading, first year survivorship (the ratio of seedlings to sown seeds) rose rapidly with slash loading, peaking at about 4-8 kg/m^2, and then declining rapidly with loadings greater than 12. Compared to the range of 4-12 kg/m^2, our lowest loading, 0.2 kg/m^2, sponsored a much smaller survivorship. Indeed, S on the latter was 26 to 29 times lower for white spruce and yellow birch, respectively. This great difference in juvenile mortality rivals what is found for small seeded species on optimal seedbeds vs. thick duff (Greene and Johnson, 1998). Thus, the advantages conferred by a small amount of slash—fewer days in the summer with high surface soil temperatures; better soil moisture status—lead to dramatically greater survivorship.

Our mean survivorship values were quite ordinary; the S values we obtained for our two species were similar to those predicted by the 30 sowing experiments on mineral soil collated by Greene and Johnson (1998). For white spruce their equation, a function of seed mass, predicts 0.051, while we observed (all loadings averaged) 0.042. For yellow birch their equation predicts 0.039 while we found 0.045.

The two species have similar masses (and thus germinant sizes) and should therefore have similar mean S values (as they did). The initial rise in survivorship in our two species occurred despite the loss in available soil substrate with increasing loading. With survivorship defined as S/p, the modal slash loading was displaced toward a higher loading (12 kg/m^2) with a concomitant rise in S to this mode and a rapid decline in S/p from 12 to 24 km/m^2. A likely explanation for this decline is that many seeds were trapped in the contact points between adjacent pieces of wood, and that this trapping became increasingly important from about 8 kg/m^2. That is, S declined at high loadings because of seed trapping by the woody residue rather than because of the loss in available substrate.

One other explanation is that the dense shade under high slash loadings leads to early mortality of germinants. This follows from the result that the modal survivorship for yellow birch occurred at significantly lower loadings than the mode for white spruce, and showed a lower survivorship at very high loadings. As shown by Kneeshaw et al. (2006), when small, yellow birch is less shade tolerant than white spruce. Thus, if dense shade at this early stage can cause first-summer mortality then it joins seed trapping as an important cause of mortality as loadings increase.

While it is well understood that there is a dramatic difference in survivorship for small-seeded species on thick duff vs. exposed mineral soil and humus, there has been far less discussion of the tremendous variation that is found for S on mineral soil and humus. Using 30 records of sowing of white spruce on optimal seedbeds, Greene and Johnson (1998) found that 98% of the recorded values ranged from 0.005 to 0.333. This range is not much greater than what we found here with spruce for loadings <24 kg/m^2 (i.e. non-O survivorship values). While Greene and Johnson (1998) did not examine the effect of loading (and most of the authors of those 30 studies did not mention the amount of woody debris on their plots), we have in this study uncovered a major source of that tremendous variation in survivorship.

Interestingly, the optimal slash loading for regeneration, roughly 2-12 kg/m^2, is similar to what is found naturally following cut-to-length harvesting. The typical amount of slash remaining prior to any removal to the landing is in the range 5-15 green kg/m^2 (e.g. Lieffers and Van Rees, 2002; Relvic et al. 2007; Alam et al., 2012). By contrast, after conventional whole-tree harvesting, the loadings range as 0.4 to 10.4 with an average of 3 kg /m^2 (the dry weight measures in the review of Thiffault et al., 2014, are converted here to green weight by doubling). Where a small clearcut is created after the autumnal abscission of seeds during a mast year for a commercial species, and where disruption of the forest floor by equipment is sufficient to ensure an adequate proportion of good seedbeds, a cut-to-length operation would lead to optimal juvenile survivorship (Greene et al., 2002).

The removal of forest harvest residue for bioenergy can be a sustainable use of wood biomass. However, in some areas and under some conditions, maintenance of soil fertility and biodiversity, transport costs, or a combination of these concerns are increasingly considered when deciding how much slash should be retained (Lal et al., 2011, Abbas et al., 2011). The minimum amount of slash retention required in some countries and states is 2 kg/m^2. It has been argued this is not enough for fungal diversity (Nordén et al, 2004), the non-commercial flowering plants needed by pollinators and frugivores (McCavour et al., 2014), or ecosystem services generally (Wei et al., 2012). This paper adds the argument that an average of only 2 kg/m^2 will lead to minimal to poor regeneration by the small-seeded species typical of the circumboreal forest. Further work replicating these trials, for seeds of smaller and larger size would help with decision making in slash management. For example, in areas where one wishes to manage for maintenance of a small seeded metapopulation, or promotion of a certain species, selective harvesting methods and selective slash retention policies may help achieve these goals.

3.6 Figures

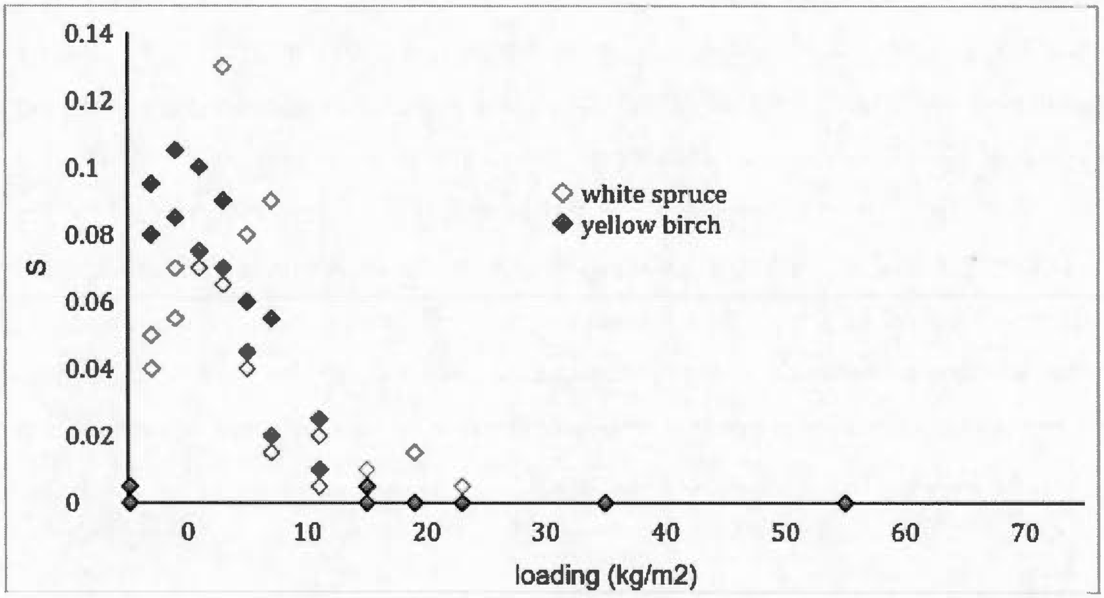


Figure 3.1. First growing season germination and survivorship (S) as a function of slash loading (kg/m^2).

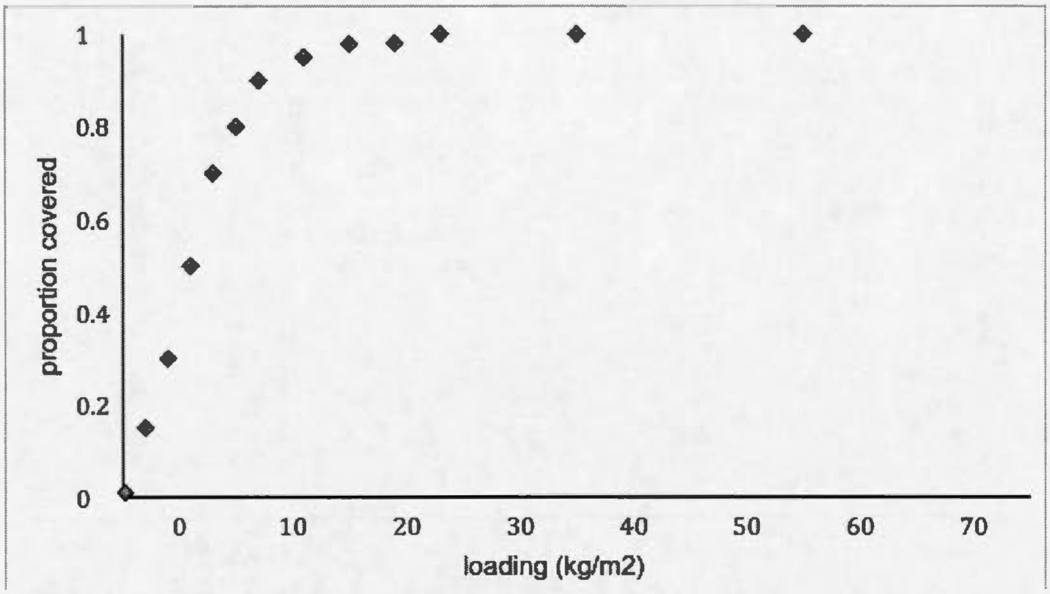


Figure 3.2. The increase in the mean proportion of the ground covered by wood as a function of slash loading (kg/m^2).

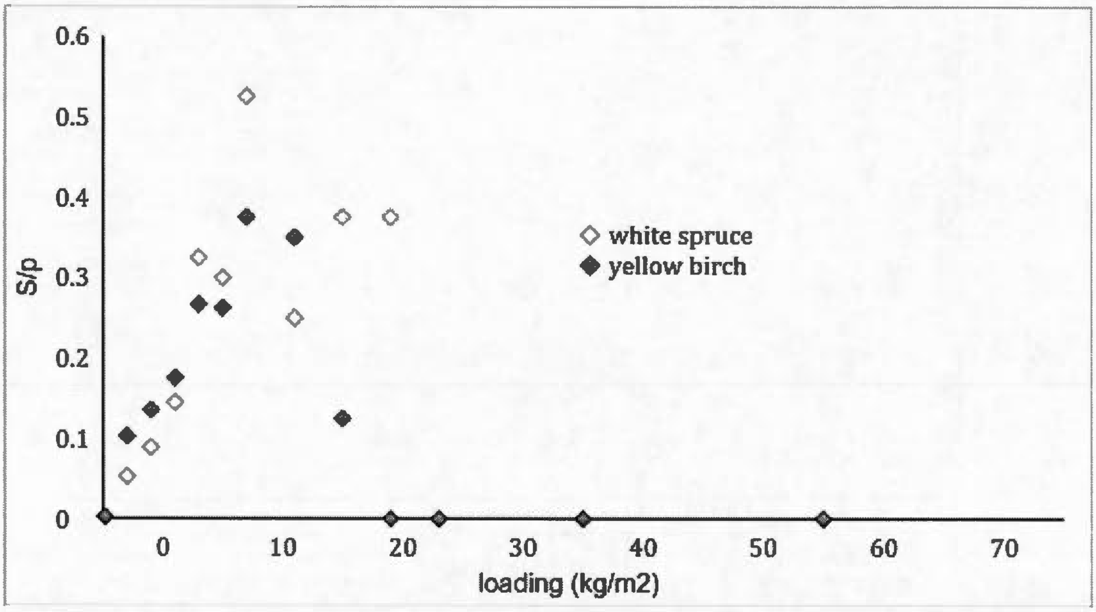


Figure 3.3. The ratio of mean survivorship (S) to the proportion (p) of the ground covered by wood as a function of slash loading (kg/m^2).

GLOBAL CONCLUSIONS

The main reasons to remove slash until recent years have been to (1) facilitate site preparation and planting and (2) reduce the fire hazard (Fernandes and Botelho, 2003). These accumulated residues in North America have seldom been taken for energy generation because of the low market value relative to high transportation costs (Miller et al. 1987; Spinelli and Visser, 2009); instead slash was often burned at the landing (Jones et al., 2010). However, societal demand for sustainably sourced energy (relative to fossil fuels and large dams of significant impact) and emerging technologies that allow on-site conversion to biofuel (greatly reduceing transportation costs as bulk density is reduced), may lead to to a more widespread utilization of slash as a biofuel (Li et al., 2015; Han et al., 2004). That is, the [presently low] efficiency of residue removal during whole-tree harvesting (Briedis et al., 2011) may well increase sharply in the near future. Until the technology needed to transfer, store and temporally manage the abundant energy derived from wind, wave and solar is fully developed there may be heightened demand for slash removal from mills, factories, businesses and residents who wish to convert slash to electric power, or use it for residential and commercial heating.

While there are these above arguments for slash removal from the harvest block, as we saw in the Global Introduction, there are also numerous papers that have shown the benefits of slash retention. These include enhanced diversity and cover of understory plants (Berger et al., 2013), improved tree growth due to enhanced nitrogen and phosphorous (Smith et al., 1986), increased beetle and fungal diversity (Gunnarsson et al., 2004), and shelter for many small mammal species (McCay, 2000).

This dissertation augments the literature on the beneficial aspects of residue retention, and in particular, is the first to investigate the effects of spatially aggregated slash on soil fertility, and plant growth, flowering and fruiting. These results are the first to examine the effects of piled slash on pollination services (via enhanced reproductive output), and the ensuing effects on dependent frugivores and biodiversity. In addition, this dissertation addresses and uncovers several important sources of the variation in results and conclusions seen in the literature on soil nutrients and plant growth on sandy sites where slash is or is not retained. In Chapter 1 it was shown that on sandy sites there is a marked gradient in soil nutrient availability with distance from large slash piles out to approximately 10 m. Subsequentally, the early successional species strawberry, raspberry and pin cherry had much better growth and density near piles. Furthermore, flowering and fruit production in the cutblock was almost completely due to individuals located near piles. As canopy closure of the planted stock matrix occurs, large piles will still receive a great deal of light, and early successional species can colonize the pile tops as they begin to decompose and densify. Indeed, at the 16-year-old study site cherry flowering was almost entirely restricted to slash piles and was even more robust than at the younger site. Pollinators and frugivore populations in an industrial forest landscape, or in any fragmented metapopulation experiencing population segregation, will be greatly dependent upon the presence of aggregated slash given that almost all high-latitude commercial tree species are both wind-pollinated and wind-dispersed, and industrial plantations are often located in areas with well-developed transport and market opportunities- regions typically possessing fewer habitat corridors. Migrant pollinators, such as the monarch butterfly, and many birds are also highly dependent on resource connectivity.

Clearly, more studies are required to confirm that aggregated slash does indeed have these effects. Questions remaining include: What is the rate at which the top of a pile or windrow decomposes and thus sexual recruitment can begin on top of the pile? In a truly industrial forest such as in Finland or as imagined within the Triad or CBFA concept, what is the contribution, if any, of roadsides, with their high light availability (but low nutrient status) to flowering and/or fruiting of non-plantation plants? How does the dispersal capacity of these non-plantation species (almost invariably not understood at present) interact with harvest block size and density at the landscape scale when we view them as metapopulations?

Chapter 2 was based on the same set of piles as in the first chapter but with a focus on the growth of the planted hybrid poplars. As with the early successional plants, poplar showed an exponential decline in growth with distance from pile to about 10 m. Further, the poplars near piles had larger amounts of foliar cations. There was more biomass (despite fewer trees) in blocks with slash piles retained than in blocks with no piles (despite a greater number of trees). The law of constant final yield was used to show that the enhanced growth must be due to added soil resources; we calculated that poplars near piles must have about double the nutrient availability as do stems far from piles. It was concluded that aggregated slash on-site can significantly reduce the rotation time for the entire block or lead to higher yield of fiber after the originally planned rotation period.

Much remains to be done with the issues arising from this chapter. For example, one asks: will the differences in poplar growth rates near vs far from piles continue to increase with time? The literature supports this possibility, but is specific to hybrid poplars. If so, the economic argument for retaining slash in hybrid poplar plantations is heightened. What is the optimal spatial distribution of slash for even a single competing beneficial use? For example, if we merely wish to enhance poplar growth, there must be some point in the imaginary disaggregation of slash as we trend toward a perfectly (and impossible) even dispersion of woody material where the benefit is wide-spread but ephemeral. Will this lead to any difference in yield at rotation age? Another question is: to what degree are the results presented here only valid for fast-growing species on sandy sites near aggregated slash? Almost no other studies showing a lack of effect for WTH vs cut-to-length discuss where study plots were located in relation to slash aggregations. Given that these aggregations will typically occupy only about 2% of the harvest block and, with FTW be at the block edges, there is a very good chance that none of the study plots will lie within a few m of a pile or windrow. If so, we should not be surprised that so few studies show an effect on richer soils; the sampling was not spatially realistic in relation to the likely sources of enhanced plant growth. Likewise, for characteristically slow-growing species, it may be that many of the studies showing no effect from WTH are simply of too-limited duration to discern any eventual effects.

Chapter 3 studied the recruitment of small-seeded species near the same site as the previous two chapters, again on a sandy soil. In a one-month old clearcut we collected and used size-classed slash from a large pile to create 1x1 m residue aggregations varying in loading from 0 to 60 kg/m^2. This is typical of the range of residue found at a small scale among and within harvest blocks, although with a volume well below what would be found in a single traditional slash pile. In each aggregation we sowed seeds of yellow birch and white spruce, hypothesizing that survivorship would rise with loading due to improved water retention up to a maximum and then decline as (1) trapping of seeds precluded contact with the mineral or duff substrate, and (2) the increasing shade led to higher mortality of germinants. The two species showed a similar response, with a maximum survivorship occurring at 4 (birch) or 8 (spruce) kg/m^2. Broadly, the optimal range for seedling establishments was for loadings between 2-12 kg/m^2, which is quite similar to the range of mean block-wide values reported following cut-to-length harvesting.

There is much follow-up work to be done for this chapter. How much of the varying literature on slash effects on recruitment actually makes an attempt to discuss, or mention, slash as a quantifiable loading? Do the smallest and largest loadings support the conclusions of Chapter 3? As a more esoteric study, it would be useful to actually observe seeds being trapped among the woody pieces in large loadings. Finally, a study of soil moisture in relation to a range of quantified loadings among very nearby plots is needed to further support the argument that recruitment is poor with no or little slash present.

The literature has pointed to studies showing significant or no beneficial effect but can make what can be characterized as an educated guess for the minimal loading at the scale of a harvest block. Meanwhile, the issue of the spatial distribution of that loading has not been seriously entertained except for McCavour et al. (2014). What is the best arrangement and amount of retained slash? Clearly, that depends on the purpose for the retention. However, with a further shift towards ecosystem based management, there will be increased interest in tools and data that will help incorporate all aspects of slash management. For example, we could begin by postulating what the ideal prescription for the reproductive success of early successional flowering plant species should be. Given a sandy site with a fast-growing (short rotation) plantation species the prescription would be full retention of woody residue, not with "beehive" piles (needlessly tall) nor traditional windrows (too narrow to preclude canopy closure); but rather with *wide, shallow* windrows. The width should be about 1.5 times the expected crown diameter of a plantation stem at rotation age (to slow canopy closure) and with a depth sufficient to retard asexual regeneration by competing stems; perhaps 0.5 m deep. The windrows would still facilitate the movement of planters throughout the cutblock. Thus, initially the early successional angiosperm species would be limited to asexual recruitment along the extensive margins of these windrows but would within about a decade begin to colonize the decomposing slash surface itself via seed.

The merits of this suggested approach are that it (1) maximizes the area covered by residue (although it would still be a small fraction of the block); (2) provides habitat for the early successional fruiting plant species and thus for the pollinators and frugivores (much of the animal diversity) dependent on them; (3) allows for easy access for planters; (4) provides shelter or substrate for numerous animal (reptiles, mammals) species and fungi; (5) creates fuel loadings that would be near but below the typical maximum permitted by most jurisdictions; (6) increases the number of planted stems near the [increased] fertile edges of the aggregated slash rows, and thus-via growth enhancement of a greater number of stems- further shortens the rotation time on low fertility sites; and (7) would allow for more complete decomposition of the residue over a short rotation, again shortening the rotation time.

Contiguously aggregated residue (slash piles; windrows) is important as shelter for many small mammal and reptile species and some lichen groups (Manning and Edge, 2008, Sillet et al. 2000). Additionally, the flower and fruit resources important to many animals (Newmaster et al., 2007; McCavour et al. 2014) will be promoted by a spatial aggregation of slash due to increased light and the concomitant local increase in soil fertility, because these aggregations are concentrated nutrient sources and areas of open canopy.

Likewise, long moderately high windrows may be the optimal configuration for increased crop tree growth (see Figure 4.1). The optimal allocation of slash that permits the enhanced growth reported by McCavour et al. (2014) is not yet understood (but will be modelled in a subsequent paper). Clearly though, very large piles may be unnecessary for enhanced tree growth for very short rotation species, given how slowly higher portions of the pile decompose.

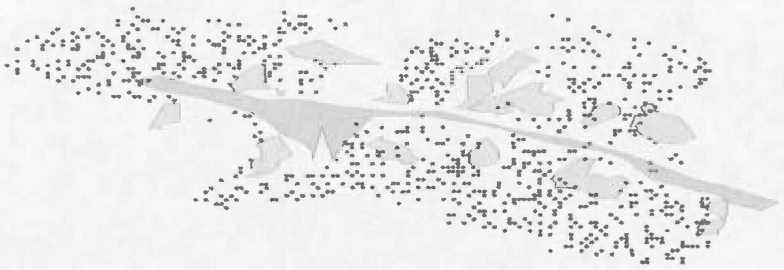
It is instructive however to consider which species or interests would be deleteriously affected by this scenario. This scenario would not permit any extraction of residue for use as biofuel. This may be less desirable in areas close to co-generational facilities or in regions where the negative impact from using fossil fuels to power pulp or timber mills is very high. Small-seeded species that cannot recruit asexually (e.g. almost all conifers and some flowering plants) would have very low densities, as seed trapping or shading in the windrows would preclude establishment, as would the dry soil located away from the windrows. Thus, it would be impossible to augment planting with naturally-recruited stock of commercially valuable conifers outside of a mast year. This scenario would also not be the best array of wood debris for the less vagile fine wood-dependent species such as the many invertebrates that benefit more from a dispersed distribution of slash.

By contrast, if a manager opts for elimination of small-seeded species for reduced cost of operational competition abatement, this could be achieved with retention of more than 12 kg/m^2 (Harrington and Schoenholtz, 2010; present study) of dispersed slash. Presumably, an even distribution of slash would also provide the greatest benefit in the first few years for soil diversity, C, or for uniform enhanced growth of planted stock.

The solution to this irreconcilability is to regard slash retention as a management tool. Both within and among blocks, there could be variation in the amount of residue removed as well as in the spatial distribution of retained slash. Tree biomass yield, or maintenance or amelioration of soil fertility, or C sequestration, or a specific compromise, could be selected for with a site-specific spatial pattern of harvest residue. For example, if selection is for red-listed or sensitive invertebrate species, a diversity of small-seeded non-commercial plant species, or for natural regeneration of small-seeded crop trees, rather than maintence of all species or services, a spatially dispersed retention of 4-8 kg/m^2 is called for (Gunnarsson et al., 2004; Russell et al., 2004; Wei et al., 2012; MacLean et al., 2015; present study). In effect, this prophylaktikós approach would be a cut-to-length harvest with- in some cases- a subsequent removal of a small amount of the residue.

Managing forests for biodiversity, ecosystem services and biomass yield will increasingly require a holistic strategic environmental assessment (pre-“project”) approach. Varying the quantity and spatial distribution of retained slash to meet desired outcomes is a potentially valuable decision tool that could help managers design and implement initial studies, forest plans and environmental assessments and meet sustainable forest management practice guidelines, policy requirements, and regulations.

Site 1



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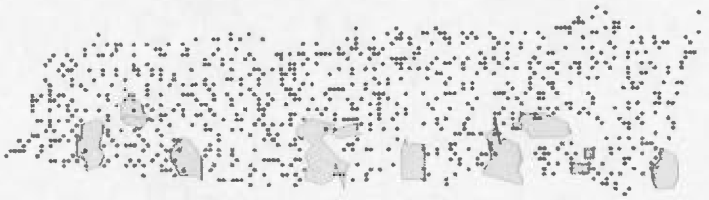

Site 3

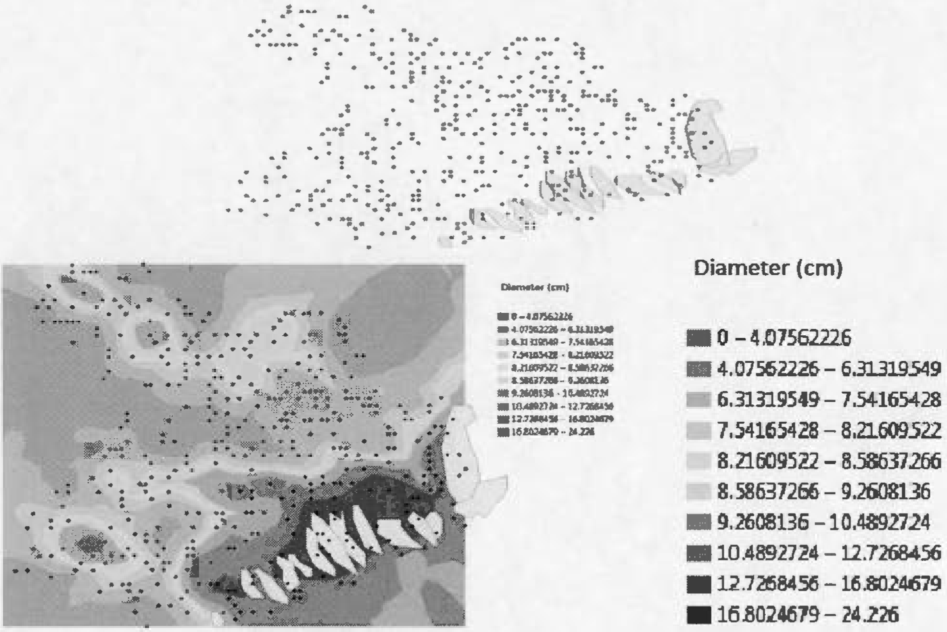

Figure 3.4. Geospatial visualization of Riviere-aux Rats sites.

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