

EXPERIMENTAL STUDY OF THE EFFECT OF THE INVASIVE SHRUB  
*FRANGULA ALNUS* ON THE GROWTH OF PLANTED UNDERSTORY TREE  
SEEDLINGS AND HERBACEOUS PLANTS

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Caroline Hamelin, candidate for the degree of Master of Science in Biology, has presented a thesis titled, ***Experimental Study of the Effect of the Invasive Shrub Frangula Alnus on the Growth of Planted Understory Tree Seedlings and Herbaceous Plants***, in an oral examination held on May 30, 2016. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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## Abstract

Glossy buckthorn is an invasive exotic shrub which is efficient at colonizing both open and forested habitats, and may impede native tree and forest herb growth. Buckthorns growing in an open field and in the understory of a hybrid poplar plantation were compared. It was found that buckthorn is capable of allometric plasticity, which may explain its invasion success in both environments. Two experiments were done to test the effect of buckthorn on tree seedlings and herbaceous plants, all planted in spring 2014 in the understory of a hybrid poplar plantation invaded by buckthorn. Both experiments had two treatments: 1) herbicide applied in fall 2013; 2) control. The objectives were to: 1) test the presumed negative effect of buckthorn on tree seedling and forest herb growth, 2) determine if this effect differed for tree species with different shade tolerances and edaphic requirements (sugar maple, red oak) and three forest herb species (*Asarum canadense*, *Sanguinaria canadensis* and *Polygonatum pubescens*), and 3) determine if the type of hybrid poplar clone canopy influenced this effect. After two years, tree seedlings had reduced diameter and height increments under buckthorn. A negative effect of buckthorn was also observed on forest herb survival and growth after one year. This effect varied among species, suggesting eventual changes in understory flora composition. Clone canopy did not have any effect on environmental variables or tree seedling and forest herb growth. Buckthorn reduced light availability, but had no effect on soil moisture or nutrient availability. Shading by buckthorn appears to cause the negative effect observed. Consistent with sugar maple's requirements, its diameter growth was explained primarily by edaphic variables (soil humidity, soil K), and secondly by buckthorn biomass. Red oak growth was explained primarily by buckthorn

biomass, and secondly by understory vegetation biomass. Although shade-tolerant species (sugar maple) may be able to grow in the presence of buckthorn, other species with higher light requirements (red oak) may have large growth reductions and have difficulty overtopping buckthorn. These results support rapid reforestation actions after buckthorn removal, by plantation or under-planting, to regenerate shelterwood cuts and low density early successional forests, in order to outgrow buckthorn and ensure future tree recruitment.

Keywords: *Frangula alnus*; exotic species; introduced species; *Acer saccharum*; *Quercus rubra*; early successional stands; southern Québec (Canada); forest herbs

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## CHAPTER ONE: General introduction

### 1.1. Exotic invasive plant species as a threat to biodiversity

Although the negative impacts of exotic plant species on native ecosystems and biodiversity have not been as well documented or as severe as those of exotic animals (ex. zebra mussel (Ricciardi et al. 1998) and sea lamprey (Smith 1971) in the Great Lakes; cats (Frank et al. 2014) and cane toads (Shine 2010) in Australia; brown snake (Fritts and Rodda 1998) on Guam), there are still a few well-known examples of exotic plants causing problems in native ecosystems, such as purple loosestrife in North American wetlands (Thompson et al. 1987) and the water hyacinth in freshwater bodies of the southeastern United States (Villamagna and Murphy 2010). Invasive species are considered to be the second most important threat to imperiled species in the United States after habitat destruction and degradation and they are held as a cause, at least in part, for the listing of 57% of the endangered species in the United States (Wilcove et al. 1998). In addition to ecological impacts, invasive species can engender serious economic consequences by inducing shifts in species abundance to the benefit of species of lower economic value, or by altering ecosystem processes and delaying plant succession, lowering forest productivity (Fagan and Peart 2004).

However, the negative effects of exotic plant species are often controversial. A good example is the purple loosestrife, for which biological control (with introduced insect species) was implemented in Canada and in the United States (Lindgren 2000; Katovich et al. 2001) to reduce its abundance in wetlands, based on the untested hypothesis of its negative impact (Hager and McCoy 1998). Several authors have challenged the validity

of the assumption that purple loosestrife was ever a threat (Anderson 1995; Hager and McCoy 1998; Farnsworth and Ellis 2001) and explained the adverse scientific, social, economic and ecological consequences that this case has had (Hager and McCoy 1998).

This ambiguous situation is probably not unique to purple loosestrife. In Québec, a recent study found that 123 plant taxa deemed not to be noxious by a panel of experts, are nonetheless listed on at least one American state's threatening plant species list (Lavoie et al. 2014). Conversely, for 87 plant species that the panel identified as threatening in Québec, 42 did not appear on any such lists in the United States. Moreover, there is also evidence that rapidly spreading and abundant exotic species are not necessarily noxious for native ecosystems. Ricciardi and Cohen (2007) have not found any relationship for exotic species between their rapidity of spread and their effect on native species. In some cases, a new species will be integrated into the ecosystem without producing significant changes (Houlahan and Findlay 2004; Mills et al. 2009). The "passenger" hypothesis suggests that in some cases, exotic species may only be taking advantage of the current conditions that are disadvantaging native plants, as opposed to being part of the problem as "drivers" of the changes (MacDougall and Turkington 2005).

Scientifically investigating if invasive plant species have real negative effects on native ecosystems is important because their control is expensive, and therefore resources should be allocated in priority to control species for which a negative effect has been experimentally shown. Control actions can have unpredictable results; they may harm native species or even increase the spread of other invasive species (Westman 1990; Kettenring and Adams 2011; Shields et al. 2015). Radical control actions may also face social disapproval because of their adverse effect on landscape aesthetics. Control actions

should therefore be carefully planned and only directed toward species proven to have a significant negative effect.

## 1.2. Glossy buckthorn, an exotic invasive shrub

Glossy buckthorn (*Frangula alnus* Miller, syn. *Rhamnus frangula* L.) is an exotic shrub that is now dominant in several ecosystems of Eastern North America (Fagan and Peart 2004). It is native to Eurasia and Northern Africa (Godwin 1943) and was probably introduced to North America for ornamental purposes. This species was first observed in North America in southern Ontario in 1898 (Catling and Porebski 1994). After a particularly rapid spread period from the 1970s to the 1980s, its current distribution range is from Nova Scotia (East) to eastern Saskatchewan (West) and South to Idaho, Colorado and North Carolina (USDA 2014a; Canadensys 2014).

As seems to be the case for many invasive species, glossy buckthorn appears to be a generalist (Mills et al. 2012) in terms of its edaphic (Godwin 1936; Godwin 1943; Mills et al. 2012), climatic (Guinochet and De Vilmorin 1973) and light conditions (Sanford et al. 2003) requirements, as well as in terms of the forest stands in which it occurs (Schoeb et al. 2012). Its invasion success seems to be due to its low ecological requirements, and to a set of traits it shares with many invasive plants.

First, glossy buckthorn has an extremely abundant, frequent and early seed production, allowing the creation of large soil seed and seedling banks (advanced regeneration) in forests (Godwin 1936; Godwin 1943; Burnham and Lee 2010; Mills et al. 2012). The seeds of glossy buckthorn have a 90 to 100% germination rate (Godwin 1936), and 70%

of the seeds that a stem produces fall right underneath it, leading to seedling densities up to 100 seedlings/m<sup>2</sup> (Godwin 1943). In a study by Mills et al. (2012), glossy buckthorn seedling density exceeded more than seven times the seedling density of four native shrub species combined. The authors proposed that this important difference with native species is explained by a low accumulation of host-specific predators and pathogens that can usually limit the agglomeration of conspecific individuals (Mills et al. 2012). With this ecological advantage, it is therefore not as reliant on long-distance dispersal as native species. Nevertheless, Mills et al. (2012) observed that long-distance dispersal of glossy buckthorn is comparable to that of four native shrub species. This is probably explained by the dispersal of its seeds by several bird species, as well as mice, through the ingestion of its small fleshy fruit (Godwin 1936; Catling and Porebski 1994; Nagel et al. 2008).

Buckthorn also shows a very strong response to the cutting of its stems (Godwin 1943). Buckthorns cut down to 5 to 15 cm in height produced up to 50 suckers per plant and reached up to 2 meters in height, all in a single growing season (Reinartz 1997). In addition, spring bud-burst in glossy buckthorn occurs earlier (mid-May) and its leaves senesce and fall later (October) than many other woody species, providing the species with a longer growing season (Malicky et al. 1970; Converse 1984). Finally, it reaches relatively large dimensions for a shrub, commonly 3 to 5 m in height (Converse 1984). Today, glossy buckthorn is considered one of the most problematic woody invaders in Eastern North American forests (Webster et al. 2006).

### 1.3. Context and Research Topic

Early successional hardwood forests with partially open canopies are common throughout the deciduous forest regions of southeastern Canada and the northeastern United States. These forests mainly result from the abandonment of agriculture on marginal agricultural areas, when agriculture became industrialized and agricultural production concentrated towards the more productive soils (Domon and Bouchard 2007). Moreover, a decline in seedling abundance and stem quality, as well as a change in composition towards lower-value early successional species were noted as a result of diameter-limit cuts which were widely applied in these regions in the past (Majcen et al. 2003; Kenefic and Nyland 2005). These early successional, partially open forests are considered as “degraded” (Sokol et al. 2004; Kenefic et al. 2005), regarding their former historical composition, structure and quality.

To restore the forest cover, the reforestation of abandoned farmland (Cogliastro et al. 1990; Johnson et al. 2002) and the restoration of valuable hardwood species to poorly regenerated second growth forests (Johnson 1975; Johnson 1984; Gordon et al. 1995; Truax et al. 2000; Paquette et al. 2006; Spetich et al. 2009; Dey et al. 2012) are becoming more widespread forest management practices. Forest herbaceous species are also planted for restoration purposes (Mason et al. 2009; Boothroyd-Roberts et al. 2013a) or they are sometimes cultivated as non-timber forest products in the understory of these types of forests. However, the success of these practices may be compromised by glossy buckthorn. This shrub is capable of invading both open areas and closed-forest understories (Converse 1984; Nagel et al. 2008) and it appears to have a negative effect on native tree seedlings and forest herbs (Frappier et al. 2003; Fagan and Peart 2004).

Whether or not the presence of glossy buckthorn truly has a negative effect on forest restoration (under-planting) and reforestation success is a question that needs answering. The answer will determine if control actions are necessary, and if substantial efforts need to be directed towards determining effective methods of buckthorn suppression.

Forest managers and conservation scientists are very concerned by glossy buckthorn (Converse 1984; Fagan and Peart 2004; Webster et al. 2007) because its spread is facilitated by openings in the forest canopy, even small natural gaps or gaps created by partial cutting (Burnham and Lee 2010; Lee and Thompson 2012). It is a somewhat shade-tolerant species that out competes native species in the colonization of canopy gaps, where it tends to form a very dense mono-specific stand (Converse 1984; Frappier et al. 2004; Nagel et al. 2008) limiting light availability for native tree seedlings. Additionally, when it becomes dominant, glossy buckthorn may possibly modify forest soil conditions through its uptake of resources (nutrients and water) and the addition of its litter to the forest floor. Following an invasion, dominant species composition can be shifted toward shade-tolerant species and the forest succession can be delayed or stopped, reducing the economic value, productivity and diversity of the forest stand (Fagan and Peart 2004; Possessky et al. 2000).

Buckthorn tends to form dense single-species stands in open areas, as well as in undisturbed forests with closed canopies (Frappier et al. 2003; Nagel et al. 2008; Lee and Thompson 2012). The maintenance of glossy buckthorn cover in shaded environments appears to be predominantly attributable to its high reproduction capacity and its high germination and growth rates (Mills et al. 2012). However, once the seedling stage is

over, and once a stand is established, no study has explained the successful persistence of buckthorn in understories and its similar efficiency in both environments.

A few studies have investigated the negative effect of buckthorn on forest understory tree seedlings and forest herbs. In forest environments and plantations, a higher basal area of glossy buckthorn has been associated with lower native tree seedling densities and growth, lower herbaceous plant cover, lower species richness and shifts in dominant vegetation favoring shade-tolerant species (Frappier et al. 2003; Fagan and Peart 2004). These results suggest that the seedlings of different tree and different forest herb species may have different levels of tolerance to competition from buckthorn. A better knowledge of the differences in tolerance to buckthorn competition among species would help guide the selection of the more tolerant species for planting.

In contrast with the studies cited above, other authors did not detect any relationships when studying similar variables, although some of them even studied potential effects over a 15-year period (Houlahan and Findlay 2004; Mills et al. 2009; Owen Koning and Singleton 2013). This discrepancy perhaps indicates that the effect of buckthorn varies depending on the region and on the ecosystem (Frappier et al. 2003). Several authors have emphasized the importance of doing regional studies to evaluate the effects of invasive species (Frappier et al. 2004; Ricciardi and Cohen 2007; Nagel et al. 2008). Also, some types of forest have been shown to be more susceptible than others to invasion by buckthorn (Owen Koning and Singleton 2013) and the composition of a forest in terms of canopy trees may influence the effect of buckthorn on the forest understory. Control actions aiming to reduce buckthorn abundance or to eradicate it have taken place both in Canada and in the United States. However, research on the effects of

buckthorn has been conducted mostly in the United States, in New England pine-mixed forests (part of the Northern Hardwoods forest region), and little information is available on buckthorn effects in other ecosystems.

Southern Québec is a region of Canada that is most vulnerable to invasive species, because of its southern location (relatively warm climate and gateway for new invasive species migrating north from the United States and from Ontario) and the high fertility of its soils. In southern Québec, early successional, partially open hardwood forests and tree plantations appear to be particularly likely to be invaded by buckthorn. Early successional hardwood forests cover a vast area in the Northern Hardwoods forest in the United States, as well as in Canada in the equivalent Great Lakes – St. Lawrence forest region (Rowe 1972). This wide combined forest region covers most of southeastern Canada (Ontario, Québec, Maritimes) and the northeastern United States (Minnesota, Wisconsin, Michigan, New Hampshire, Maine, Vermont, northern New York) (Johnson et al. 2002). Research on buckthorn in southern Canada is lacking, as well as research on the effect of buckthorn under partially open, early successional hardwood forests, and under plantations.

While most studies examining the effect of buckthorn focussed on the response of native tree seedlings, only a few have included native forest herbs. Mason et al. (2009) observed that the effect of woody invasive species is generally stronger on herbaceous plants than on other plant forms. The study of this vegetation stratum could thus provide a more accurate and comprehensive assessment of the effect of buckthorn on the whole forest understory. From a conservation perspective, because buckthorn is capable of invading humid and low-nutrient sites, where a large number of endangered plant species

also occur (Catling and Porebski 1994), information on the effect of buckthorn on forest herbs may allow a better prediction and prevention of the potential damages to the ecosystem.

#### 1.4. Testing the effect of buckthorn

Tree seedlings and forest herbs (both nursery produced) were planted under control and herbicide (buckthorn removed) treatments in the understory of a mature hybrid poplar plantation (15<sup>th</sup> growing season starting in spring 2014), naturally invaded by buckthorn. This experimental design offers a very uniform environment in terms of tree stem size and systematic horizontal spacing (structure). Structural uniformity is also due to the trees all being hybrid poplar clones (genetically identical), which makes the canopy very homogenous (no effect of canopy species composition). Several factors were controlled (transplantation date, deer exclusion), and several factors were measured (canopy openness, soil nutrients, canopy tree biomass, understory vegetation biomass, buckthorn density and biomass). The understory environment (light, leaf litter, soil moisture, soil nutrients) of this plantation is comparable to that of natural early-successional or partially open forests common within southern Québec (Boothroyd-Roberts et al. 2013b).

The study site has a recent and precisely known disturbance history. Before the establishment of the hybrid poplar plantation, the entire plantation area was an abandoned farm field dominated by herbaceous vegetation (old-field vegetation). Site preparation for planting consisted of ploughing, disking and removing all abandoned field vegetation by herbicide (glyphosate) application. Since the plantation's establishment, buckthorn has

naturally invaded the plantation understory. Consequently, we know that the presence of glossy buckthorn individuals within the plantation dates back to less than 15 years. The open abandoned field immediately adjacent to the plantation contains large clusters of buckthorn shrubs, which are the likely source of the seeds at the origin of the individuals growing in the plantation.

In conducting this experiment, we used small gauge transplanted trees to simulate large seedlings, and mature forest herb transplants, which no previous field study of glossy buckthorn has done. Using transplants meant that all tree seedlings and forest herbs had a similar age, size and cultivation history at the time of plantation, removing the heterogeneity in age and development that exists in natural forest understory tree seedlings and herbs.

### 1.5. Research questions

In Chapter 2 of this thesis, I report the results of a study examining naturally occurring buckthorns growing in an open field and in the understory of the mature hybrid poplar plantation used in this research project. By comparing their growth and architecture, I seek to answer the following questions:

- 1) Is buckthorn growing similarly (biomass gain) both in the open and under a tree canopy?
- 2) If this is true, will adopting different architectures (allometric strategies) allow it to optimize prospection for resources, depending on the light environment in which it grows (open field vs. under tree canopy)?

The development of an appropriate architecture in reaction to the reduction of light availability under a tree canopy could be a key feature explaining the successful persistence of buckthorn in understories and its similar efficiency in both environments.

To answer these questions, we first constructed and compared allometric relationships for glossy buckthorn in both environments (open field vs. plantation understory), to verify if buckthorns growing in an open field and under a tree canopy (understory of a hybrid poplar plantation) produced a similar amount of biomass for the same basal diameter. If this is indeed the case, it implies that light conditions in the two tested environments are equally suitable for buckthorn to express its full growth potential. We also tested if the height of buckthorns from both environments were significantly different, for a similar biomass produced. If the heights are different, it shows that glossy buckthorn is capable of a certain allometric plasticity in its architecture.

An objective of Chapter 2 was also to produce predictive allometric relationships of buckthorn aboveground biomass using basal diameter of buckthorn stems as predictor. I used one of these allometric relationships in Chapter 3.

In Chapter 3 of this thesis, an experimental manipulation is presented, testing the effect of buckthorn on the growth of tree seedlings planted in the understory of a mature hybrid poplar plantation. In Chapter 4 of this thesis, a similar experiment is presented, testing the effect of buckthorn on the growth and survival of forest herb plants planted in the same hybrid poplar plantation.

The following questions are addressed in Chapters 3 and 4:

- 1) Does buckthorn impede the growth of tree seedlings (Chapter 3) and forest herbs (Chapter 4) planted in the understory of a mature hybrid poplar plantation naturally invaded by buckthorn?
- 2) Are there differences in this effect in two tree species that differ in their tolerance to shade and in their edaphic requirements (sugar maple and red oak; Chapter 3), and in three species of forest herbs (wild ginger, bloodroot and Solomon's seal; Chapter 4)?
- 3) Does the type of hybrid poplar clone forming the canopy (5 clone types tested in the tree seedling experiment (Chapter 3); 2 clone types tested in the forest herb experiment (Chapter 4)) influence the effect of buckthorn on the growth of the planted tree seedlings and forest herbs?

Answering these questions of fundamental and applied nature will help us understand the effect of glossy buckthorn on forest understory native species, such as tree regeneration (seedlings) and understory forest herbs, and provide support for a decision on the efforts that should be allocated to control buckthorn, as well as to help to develop specific management practices to limit its abundance and propagation.

## **CHAPTER TWO: Comparing glossy buckthorn's allometric strategies in open and understory environments**

Hamelin, C., Gagnon, D. and Truax, B. 2015. Aboveground biomass of glossy buckthorn is similar in open and understory environments but architectural strategy differs. *Forests* 6: 1083-1093 (<http://www.mdpi.com/1999-4907/6/4/1083/pdf>).

### 2.1 Introduction

Glossy buckthorn (*Frangula alnus* Miller; syn. *Rhamnus frangula* L.) is an exotic invasive shrub that is now dominant in several ecosystems in Eastern North America (Catling and Porebski 1994). It is a cause for great concern among forest managers and conservation scientists, because its spread and growth are facilitated by openings in the forest canopy, even partial ones, resulting from cutting and thinning operations (Burnham and Lee 2010; Lee and Thompson 2012). Buckthorn is a somewhat shade-tolerant species that out-competes native species, especially in the colonization of canopy gaps. It tends to form dense single-species stands in open areas, as well as in undisturbed forests with closed canopies (Converse 1984; Frappier et al. 2003; Nagel et al. 2008).

In their strategies to obtain resources in the most efficient way, native and exotic trees and shrubs are constrained by a trade-off between a rapid growth rate in open environments and survival in understories. They can either be efficient at one or the other, but not both. Sanford et al. (2003) observed that buckthorn is subject to this trade-off, invalidating the hypothesis of a release from this constraint, to explain its successful invasion of both open environments and understories. Several explanations have been

proposed for this question. An explanation is that the abundant, precocious and bird-dispersed fruit (seed) production of glossy buckthorn allows for the creation of large seed and seedling banks (Godwin 1936; Godwin 1943; Burnham and Lee 2010; Mills et al. 2012). Indeed, Mills et al. (2012) observed seedling densities for glossy buckthorn exceeding more than seven times that of four native shrub species combined. These high seedling densities would lead to dense stands, despite a lower survival observed in the understory (Sanford et al. 2003). Moreover, the seeds of glossy buckthorn have a high germination rate, and buckthorn has low ecological requirements (Mills et al. 2012) and a rapid growth rate (Godwin 1943; Sanford et al. 2003; Powell et al. 2011). Thus, the maintenance of glossy buckthorn cover in shaded environments appears to be predominantly attributable to its high reproduction capacity and its high germination and growth rates (Mills et al. 2012).

However, once the seedling stage is over, and once a stand is established, is buckthorn relatively shade-tolerant and growing similarly both in the open and under a tree canopy? If this is true, will adopting different architectures (allometric strategies) allow it to optimize prospection for resources, depending on the light environment in which it grows (open field vs. under tree canopy)?

In attempting to answer this question, we first constructed and compared allometric relationships for glossy buckthorn in both environments, to verify if buckthorns growing in an open field and under a tree canopy (understory of a hybrid poplar plantation) produced a similar amount of biomass for the same basal diameter. If this is indeed the case, it implies that light conditions in the two tested environments are equally suitable for buckthorn to express its full growth potential. We also tested if the height of

buckthorns from both environments were significantly different, for a similar biomass produced. If the heights are different, it shows that glossy buckthorn is capable of a certain allometric plasticity in its architecture. The development of an appropriate architecture in reaction to the reduction of light availability under a tree canopy could be a key feature for the successful persistence of buckthorn in understories and to its similar efficiency in both environments.

## 2.2 Methods

### 2.2.1 Study site

The study compares buckthorn individuals growing in the understory of a mature hybrid poplar experimental plantation and in the adjacent open field (40 m apart) located at Sainte-Catherine-de-Hatley, in Southeastern Québec, Canada (Lat. N 45.27; Long. W - 72.05), at 320 m of elevation. In the vegetation zone where the study site is located (2c-T), the most common forest cover on mesic sites is sugar maple (*Acer saccharum*) with basswood (*Tilia americana*) (Gosselin 2007). Glossy buckthorn was first observed in the region in 1963 (Louis-Marie herbarium) and it is now dominant in many areas and represents a serious concern for forest managers.

The plantation was established in 2000 (15 years ago) on privately-owned abandoned farmland. The site was prepared in 1999 by ploughing and disking of the plantation area, and by removing the early-successional vegetation (Truax et al. 2012). In spring 2000, hybrid poplar cuttings were planted, followed by an application of glyphosate herbicide over the entire plantation area in June 2000, and only between the rows in June 2001, to

eliminate reappearing abandoned field vegetation (Truax et al. 2012). The plantation was invaded by glossy buckthorn during the following 15 years (verified by counting growth rings of harvested stems), through seeds dispersed from the adjacent open field.

The plantation follows a randomized block design, with 3 blocks and 9 hybrid poplar clones. It covers approximately 0.5 hectare (111 m x 40 m). Hybrid poplars were spaced 3 m apart along rows spaced 4 m apart, for an initial density of 833 stems/hectare (Truax et al. 2012). The average diameter at breast height of the hybrid poplars was  $23.5 \pm 5.6$  cm (mean  $\pm$  s.d.) in 2014, and the basal area of the plantation was 22 m<sup>2</sup>/ha. Hybrid poplar biomass measurements required the harvesting of 30 trees (15 in 2007, and 15 in 2012) (Truax et al. 2012; Truax et al. 2014). The canopy openings resulting from the harvesting have created light conditions comparable to that of woodlots where owners have thinned the forest, or where small-scale wind throw or ice storm damage has occurred. The average canopy openness of the plantation, a proxy for light availability, was 32% in 2014 (determined by the analysis of hemispherical photographs, using Gap Light Analyzer software v. 2.0 (Frazer et al. 1999)). A natural gradient in glossy buckthorn density, measured in 2014, from block 3 (7 stems/m<sup>2</sup>; buckthorn most likely first invaded plantation through this block) to block 1 (2 stems/m<sup>2</sup>) is associated to an opposite gradient of hybrid poplar yield (canopy closure) and soil fertility. In the plantation understory, as well as in the open field, no management of buckthorn was done and natural density is preserved. The open environment is an abandoned field adjacent to the plantation, where buckthorn forms scattered and very dense monospecific thickets of highly ramified individuals.

### 2.2.2 Sampling, regression procedures and data analyses

Glossy buckthorn of different sizes were collected from July to August 2014 in the understory of the plantation (44 samples; Figure 2.1), and in the open field (22 samples). Sampling in the plantation was done at least 4 m from the plantation edge to reduce edge effects. Basal diameter and total height of each sample were measured, and age was estimated by counting the annual growth rings at ground level (Figure 2.2). Samples were cut at ground level and weighted immediately on site (wet weight), in separate bundles of stems with branches and bundles of leaves. A subsample of all wet samples were dried in a drying oven to obtain dry weight, and used to calculate total dry biomass for each sample.

An aboveground predictive equation of biomass (woody parts plus leaves) ( $Y$ ) was developed for each environment (open field and plantation), using basal diameter, age or height as predictor variables ( $x$ ) (allometric relationships). Regression model selection was based on the Akaike information criterion (AIC) and on the fit of the model ( $R^2$ ). All selected regression models were power functions.

A series of non-parametric ANCOVAs was performed to determine if there was a significant statistical difference between the relationships obtained from buckthorns growing in the plantation and buckthorns growing in the open field. The ANCOVAs tested age, basal diameter or height, as a continuous covariate, and the environment (open field or plantation understory), as a main categorical effect on the aboveground biomass or height. Non-parametric ANCOVAs were chosen because the data did not have a

normal distribution. All analyses were done using the R program package (R Development Core Team, version 3.1.2 (2014-10-31)).



Figure 2.1 Hybrid poplar plantation understory with abundant glossy buckthorns



Figure 2.2 Harvested buckthorn stem cross section showing growth rings

### 2.3 Results

We developed two aboveground predictive equations of total aboveground dry biomass (woody parts plus leaves), one for buckthorn in open fields, and one for buckthorn under plantation canopy. We also developed a general regression model for buckthorn, using data from buckthorns from both light environments (Table 2.1).

Table 2.1 Allometric relationships between basal diameter of buckthorns, as the predictor variable ( $x$ ), and total aboveground biomass, as the response variable ( $Y$ ), in open field and plantation understory light environments

Environment	Buckthorns harvested	Age range (years)	Basal diameter range (mm)	Height range (cm)	Model $x$ = basal diam. (mm) $Y$ = dry biomass (g)	$R^2$
Plantation	44	2-14	2-82	54-620	$Y = 0.3684 x^{2.2048}$	0.93
Open field	22	2-26	2-112	53-695	$Y = 0.5607 x^{2.1378}$	0.88
General	66	2-26	2-112	53-695	$Y = 0.2958 x^{2.2735}$	0.90

Another use of the predictive biomass equations is to calculate the biomass of glossy buckthorn in understories and open fields. As an example, in the study plantation the total aboveground dry biomass of glossy buckthorn is calculated to be 5285 kg/ha, using basal diameter data measured for all stems in sample plots, and the plantation specific regression equation (Table 2.1).

For a given age or basal diameter, the relationships describing total aboveground biomass of buckthorns in the open field and in the plantation were not significantly

different (Table 2.2, see Figure 2.3 for basal diameter and total aboveground biomass relationships).

We then tested for a difference in the height of buckthorns in the two environments. For a given age, basal diameter, or total aboveground biomass, we observed that buckthorns in the plantation have a significantly higher height than the ones growing in the open field (Table 2.2, see Figure 2.4 for age and total aboveground biomass relationships).

Table 2.2 Significance levels ( $p$  values) for the non-parametric analyses of covariance (ANCOVA) testing age, basal diameter or height, as a continuous covariate (independent variable), and the environment (open field or plantation understory), as a main categorical effect on the aboveground biomass or height (dependent variable).

Response ( $Y$ )	Predictor ( $x$ )		
	Age (years)	Basal diameter (mm)	Height (cm)
Aboveground biomass (g)	0.5025	0.1244	0.0149*
Height (cm)	0.0100*	0.0149*	
Basal diameter (mm)	0.0199*		

\* Significance at  $p < 0.05$ .

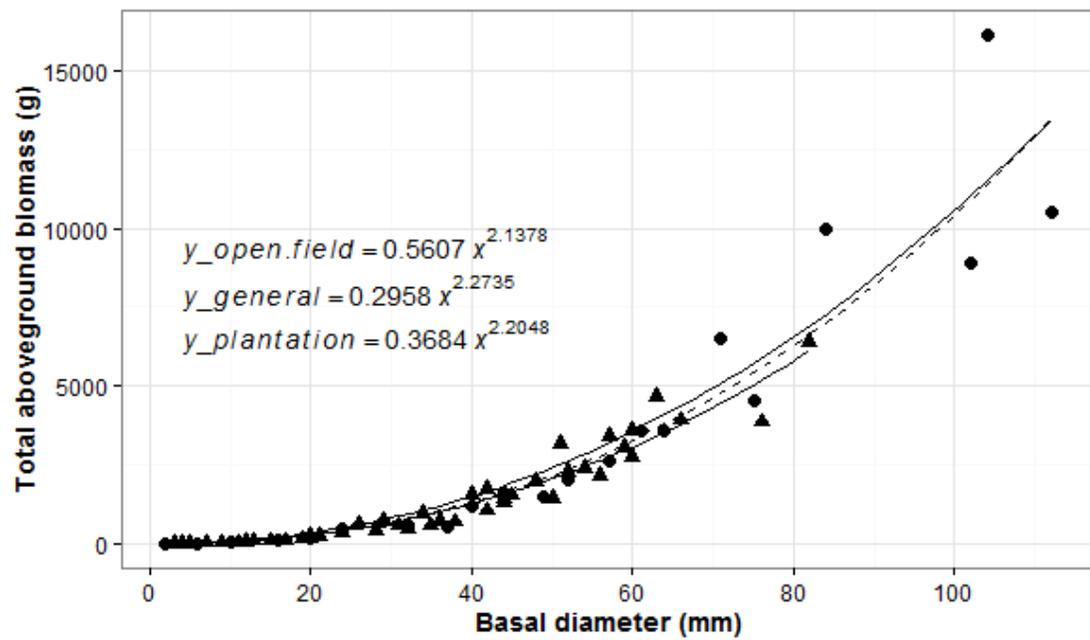


Figure 2.3 Environment-specific relationships and general allometric relationship for glossy buckthorn between basal diameter (mm) and total aboveground biomass (g). Triangle symbols = Plantation data points; Circle symbols = Open field; Dotted line = general model (plantation + open field).

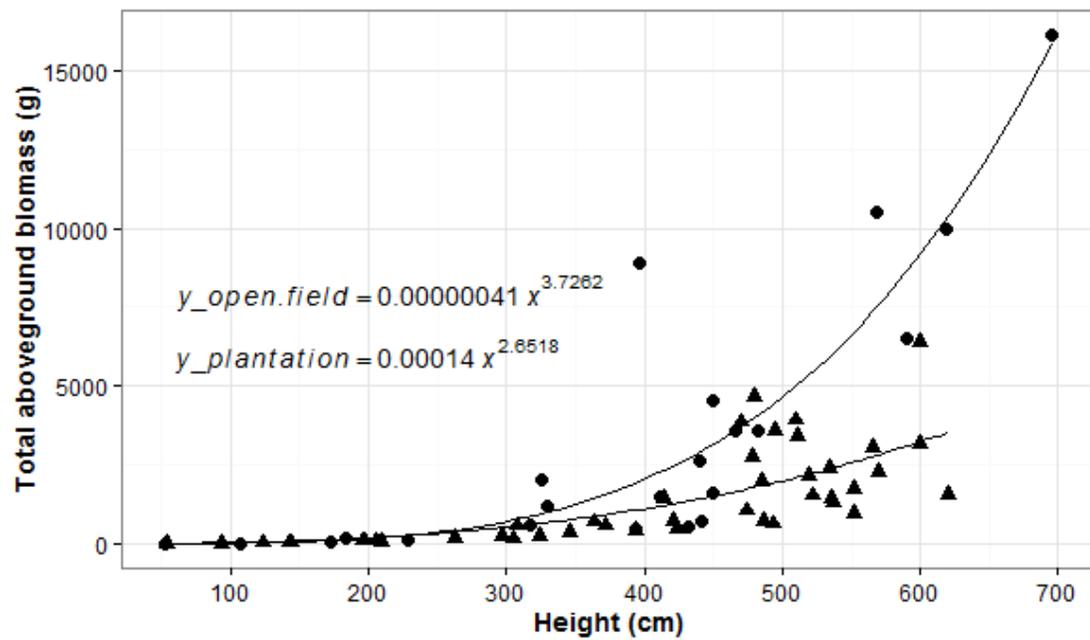


Figure 2.4 Environment-specific allometric relationships for glossy buckthorn between height (cm) and total aboveground biomass (g). Triangle symbols = Plantation data points; Circle symbols = Open field.

Therefore, at a given age, buckthorns in the plantation and in the open field will have reached a similar basal diameter and total aboveground biomass, but significantly different heights (higher for buckthorns in the plantation).

## 2.4 Discussion

Because we did not observe an increase in biomass corresponding to an increase in height, our results suggest a change in buckthorn architecture, and not simply a change in growth rates. We observed that glossy buckthorn follows two different architectural patterns that are consistent with the ones described by Charles-Dominique et al. (2012) for common buckthorn (*Rhamnus cathartica* L.), a species similar to glossy buckthorn in many respects.

Charles-Dominique et al. (2012) described common buckthorn's strategy as a trade-off between two shapes. Under a tree canopy, it develops an arborescent shape, investing mainly in a vertical structure with long modules and limited branching to reach a higher position in the canopy and access more light (see Figure 2.5). Buckthorn uses this strategy to position itself advantageously in the understory, by increasing its height even if resources are scarce, in what some authors called a "waiting phase" (Heuret et al. 2000). This state would be reversible if conditions change. In contrast, in an open area, buckthorn adopts a shrub shape, using short modules and abundant branching to take space in the shrub stratum (Charles-Dominique et al. 2012) (see Figure 2.6).



Figure 2.5 Arborescent architecture of glossy buckthorn in plantation understory



Figure 2.6 Small thicket of glossy buckthorns in open field

The similar amount of biomass produced for the two different shapes involves a different partitioning (allocation) of this biomass, in order to change buckthorn's architecture to achieve the most optimal design for capturing the light available in the two different environments. The similar production of biomass also indicates that glossy buckthorn is able, with this change in its allocation strategy, to be equally efficient in both open and shaded environments, at least up to the level of canopy closure of the plantation used for this study. The study plantation has a canopy openness of 32%, intermediate to that of an open field (with as low as 55% openness) and of naturally regenerated woodlots (second-growth forests) dominated by hardwood species (approximately 12% openness) (Boothroyd-Roberts et al. 2013b). Considering that several authors observed that light is a limiting factor in the spread of glossy buckthorn (Godwin 1943; Converse 1984; Catling and Porebski 1994), our study plantation may not have yet reached the threshold of canopy closure over which the photosynthetic performance of buckthorn is altered.

Furthermore, Sanford et al. (2003) suggested that a particularly high photosynthetic capacity of glossy buckthorn could be the characteristic that allows it to grow faster than all the other species they tested, three native and two exotic. Sanford et al. (2003) observed that buckthorn was able to maintain its leaf area ratio from a closed to an open environment, showing a good photosynthetic performance in both environments. Moreover, buckthorn benefits from an extended period of photosynthetic activity. In fact, glossy buckthorn's leaf emergence occurs earlier (mid-May) and its leaves senesce and fall later (October) than many other woody species, providing it with a longer growing season (Malicky et al. 1970; Converse 1984). These two characteristics may be

particularly significant contributions to buckthorn success when it is growing in a forest understory, where light availability during the growing season is limited (Harrington et al. 1989).

## 2.5 Conclusion

Consistent with what other authors have suggested, our results confirm that glossy buckthorn is very efficient at colonizing new habitats, whether open or forested. We observed that buckthorns growing in the open or under a tree canopy had at a same age produced a similar amount of aboveground biomass, while using two different architectural strategies. The predictive relationships developed can also be used to calculate the aboveground biomass of glossy buckthorn, a result that will be most useful to forest managers and conservation managers alike.

## CHAPTER THREE: The effect of glossy buckthorn on native tree seedlings

Hamelin, C., Truax, B. and Gagnon, D. Glossy buckthorn impedes growth of red oak and sugar maple under-planted in a mature hybrid poplar plantation (Submitted to New Forests, January 2016).

### 3.1 Introduction

Forest managers and conservationists are very concerned by glossy buckthorn (*Frangula alnus* Mill.) (Converse 1984; Fagan and Peart 2004; Webster et al. 2007), an exotic invasive shrub that is now dominant in several ecosystems in Eastern North America. Its spread is facilitated by openings in the forest canopy, even partial ones, resulting from cutting and thinning operations (Burnham and Lee 2010; Lee and Thompson 2012). It is a somewhat shade-tolerant species that out competes native species in the colonization of canopy gaps, where it tends to form a very dense mono-specific stand (Converse 1984; Frappier et al. 2004; Nagel et al. 2008) limiting light availability for native tree seedlings. Additionally, when it becomes dominant, glossy buckthorn may possibly modify forest soil conditions through its uptake of resources (nutrients and water) and the addition of its litter to the forest floor. Some authors have observed that buckthorn has an extensive shallow root system which may be highly competitive for below-ground resources (Fagan and Peart 2004), as it was observed for another exotic invasive shrub (*Berberis thunbergii*; Ehrenfeld et al. 2001). By limiting resources for tree seedlings, the regeneration of the canopy tree species can be delayed or arrested, reducing the diversity and productivity of the forest stand. Potential changes in

forest species composition may also result in a lower value for the future forest (Fagan and Peart 2004).

A few authors have investigated the effect of buckthorn on forest understory tree seedlings. In forest environments and plantations, a higher basal area of glossy buckthorn has been associated with lower species richness and shifts in dominant vegetation towards shade-tolerant species (Frappier et al. 2003; Fagan and Peart 2004). These results suggest that the seedlings of different tree species may have different levels of tolerance to competition from buckthorn. A better knowledge of the differences in tolerance to buckthorn competition among tree species would help guide the selection of the more tolerant species for planting.

According to simulations made by Fagan and Peart (2004), less than 10% of tree saplings would be able to survive under a dense cover of glossy buckthorn and a closed canopy. Several studies have also associated buckthorn presence or high basal area with lower tree seedling survival, density and growth (Frappier et al. 2003; Fagan and Peart 2004). In an experimental field manipulation in New Hampshire, two years after removing buckthorn, Frappier et al. (2004) observed an increase in tree seedling density (including red oak), but no effect of the treatment on species richness. In contrast with these results, other authors did not observe any relationship when studying similar variables, although some of them studied the effect of buckthorn over a 15-year period (Houlahan and Findlay 2004; Mills et al. 2009; Owen Koning and Singleton 2013). This discrepancy perhaps indicates that the response to buckthorn invasion varies depending on the geographical location (Westman 1990; Frappier et al. 2004; Ricciardi and Cohen 2007; Nagel et al. 2008) and on the type of ecosystem (Frappier et al. 2003).

Several authors have emphasized the importance of doing regional studies to evaluate the effects of invasive species (Frappier et al. 2004; Ricciardi and Cohen 2007; Nagel et al. 2008). Also, some types of forest have been shown to be more susceptible than others to invasion by buckthorn (Owen Koning and Singleton 2013) and the composition of a forest in terms of canopy trees may influence the effect of buckthorn on the forest understory. Control actions aiming to reduce buckthorn abundance or to eradicate it have taken place both in Canada and in the United States. However, research on the effects of buckthorn has been conducted mostly in the United States, in New England pine-mixed forests (part of the Northern Hardwoods forest region), and little information is available on buckthorn effects in other ecosystems. Southern Québec is a region of Canada that is most vulnerable to invasive species, because of its southern location (relatively warm climate and gateway for new invasive species) and the high fertility of its soils. In southern Québec, early successional, partially open hardwood forests and tree plantations appear to be particularly likely to be invaded by buckthorn.

Early successional hardwood forests cover a vast area in the Northern Hardwoods forest, the approximate equivalent of which is in Canada the Great Lakes – St. Lawrence forest region (Rowe 1972). This wide combined forest region covers most of southeastern Canada (Ontario, Québec, Maritimes) and the northeastern United States (Minnesota, Wisconsin, Michigan, New Hampshire, Maine, Vermont, northern New York) (Johnson et al. 2002). Through most of this large region, forests on relatively rich mesic sites are generally dominated by sugar maple (*Acer saccharum* Marsh.), whether they are old-growth (rarely), or more commonly second growth after logging. However, early successional forests originating from abandonment of agriculture are usually dominated

by other hardwoods species that are much less shade tolerant than sugar maple, such as red maple (*Acer rubrum* L.), poplars (*Populus tremuloides* Michx., *P. grandidentata* Michx), birches (*Betula papyrifera* Marsh., *B. populifolia* Marsh.) and ashes (*Fraxinus americana* L., *F. pennsylvanica* Marsh.). The reforestation of abandoned farmland (Cogliastro et al. 1990; Johnson et al. 2002) and the restoration of valuable hardwood species to poorly regenerated second growth forests (Johnson 1975; Johnson 1984; Gordon et al. 1995; Truax et al. 2000; Paquette et al. 2006; Spetich et al. 2009; Dey et al. 2012) are becoming more widespread forest management practices. In fact, early successional hardwood forests dominated by poplars and other intolerant species have been found to be the best stands for under-planting with red oak (*Quercus rubra* L.) (Truax et al. 2000; Truax et al. 2015). Moreover, Gardiner et al. (2004) obtained good results for Nuttall oak seedlings planted to enrich the understory of a plantation of rapidly growing native poplars. In southern Québec, over 230 000 hectares hold a potential for either under-planting or plantation of valuable hardwood species (regional forest managers, personal communications). Whether or not the presence of the invasive glossy buckthorn has a negative effect on their success is a question that needs answering. The answer will determine if control actions are necessary, and if substantial efforts need to be directed towards determining effective methods of buckthorn suppression for restoration (under-planting) and reforestation projects.

Studying invasive species is also important because their control is expensive, and therefore resources should be allocated in priority to control species for which a negative effect has been experimentally shown. Some authors have concluded that in many cases control actions were initiated against exotic species according to widespread

assumptions, and without solid evidence of their negative effect on a given ecosystem (Houlahan and Findlay 2004; Owen Koning and Singleton 2013). In Québec, a recent study found that 123 plant taxa deemed not to be noxious by a panel of experts, are nonetheless listed on at least one American State's threatening plant species list (Lavoie et al. 2014). Conversely, for 87 plant species that the panel identified as threatening in Québec, 42 did not appear on any such lists in the United States. Moreover, there is evidence that rapidly spreading and abundant exotic species are not necessarily noxious for native ecosystems. Ricciardi and Cohen (2007) have not found any relationship for exotic species between their rapidity of spread and their effect on native species. In some cases, a new species will be integrated into the ecosystem without producing significant changes (Houlahan and Findlay 2004; Mills et al. 2009). The "passenger" hypothesis would suggest that glossy buckthorn may only be taking advantage of the current conditions that are disadvantaging native plants, as opposed to being part of the problem as a "driver" of the changes (Macdougall and Turkington 2005). Lastly, control actions can have unpredictable results; they may harm native species or even increase the spread of other invasive species (Westman 1990; Kettenring and Adams 2011; Shields et al. 2015). Radical control actions have also faced social disapproval in the past years because of their adverse effect on landscape aesthetics. Control actions should therefore be carefully planned and only directed toward species proven to have a significant negative effect.

Sugar maple (*Acer saccharum* Marsh.) and red oak (*Quercus rubra* L.) are the two native tree species we selected for testing the potentially negative effects of buckthorn on tree seedlings. Both species are known for high quality timber production, their timber

being among the most valuable in Canada. At the ecological level, sugar maple is one of the dominant hardwood species in the Northern Hardwoods forest region and red oak is one of its associated species, and both species occur in the forests surrounding the study site (Godman 1992; Gosselin 2007).

Both tree species grow best on well-drained, nutrient rich soils with full sunlight (Logan 1965; McGee 1968; Phares 1971; Crow 1992; Ashton and Larson 1996; Canham et al. 1996; Beaudet and Messier 1998). However, red oak is essentially a mid-successional species, whereas sugar maple is more abundant in late-successional stands, and they both can tolerate the suboptimal conditions of light and soil resources that are often found in the understory of hardwood forests (Bazzaz and Carlson, 1982; Logan, 1965; Beck, 1970). Both species have a conservative growth pattern (determinate in the case of sugar maple (Marks 1975; Gaucher et al. 2005) and semi-determinate (Hanson et al. 1986) ("episodic or flushing" used by Dickson et al., 2000) in the case of red oak) with a relatively slow growth rate and the maintenance, under varying light conditions, of high proportional biomass and carbohydrates allocations to their root system (high root:shoot ratio) (Logan 1965; Canham et al. 1996; Gaucher et al. 2005). These traits make them relatively stress-tolerant (Kolb et al. 1990; Canham et al. 1996) and contribute to their ability to persist in the understory for many years until resources become more favorable for the sapling to recruit into the canopy (Kolb et al. 1990; Dey and Parker 1996).

However, these two species do differ in their tolerance to shade and in their edaphic requirements. Sugar maple is shade tolerant (Gaucher et al. 2005; Humbert et al. 2007) and has relatively high edaphic requirements (St Clair and Lynch 2005), while red oak is a species of intermediate shade tolerance (Bazzaz and Carlson 1982; Gottschalk 1985;

Gottschalk 1994; Humbert et al. 2007; Kolb et al. 1990; Phares 1971; Walters et al. 1993) with low to moderate edaphic requirements (Truax et al. 1994; Canham et al. 1996). Sugar maple seedlings have been observed to be very sensitive to nutrient availability (Park and Yanai 2009), whereas young planted red oaks are far less sensitive (Truax et al. 1994). Red oak can become established and form stands on very rapidly drained slopes with shallow soils, but sugar maple does not (Gagnon and Bouchard 1981), because it cannot tolerate the lack of soil moisture. Red oak is more plastic in its morphology and physiology than species that are tolerant to shade (eg. sugar maple), but less than species intolerant to shade (Bazzaz 1979; Bazzaz and Carlson 1982; Dey and Parker 1996; Humbert et al. 2007). Red oak also has a net photosynthetic rate (NPR) that is intermediate to that of species that are intolerant (higher NPR) and those that are tolerant (lower NPR) to shade (Walters et al. 1993). Sugar maple can grow under a closed canopy (Logan 1965; Bazzaz and Carlson 1982; Walters et al. 1993; Humbert et al. 2007), where it forms seedling banks that can be suppressed for decades, but still retain the capacity to respond to openings in the canopy (Marks and Gardescu 1998).

Under the partially open canopy and on the moderately fertile soil of the mature hybrid poplar plantation used for this experiment, both sugar maple and red oak are expected to grow well. The differences in shade tolerance and in edaphic requirements between the two species will allow us to assess if the effect of glossy buckthorn varies depending on the shade tolerance level and edaphic requirements of tree species seedlings.

The objectives of this study are: 1) to test the effect of glossy buckthorn on the growth of tree seedlings planted in the understory of a mature hybrid poplar plantation naturally

invaded by buckthorn, 2) to determine if there are differences in this effect in two tree species that differ in their tolerance to shade and in their edaphic requirements (sugar maple and red oak), and 3) to determine if the type of hybrid poplar clone forming the canopy (five clones tested) influences the effect of buckthorn on the growth of the tree seedlings.

## 3.2 Methods

### 3.2.1 Experimental approach

In conducting this experiment we used small gauge transplanted trees (nursery produced) to simulate large seedlings, which no previous field study of glossy buckthorn has done. Using transplants meant that all tree seedlings had the same age and cultivation history at the time of plantation, removing the heterogeneity in age and development that exists in natural forest understory seedlings. It also enabled us to focus on this particular stage of larger understory seedlings, the size of 3 to 6 year-old naturally established tree seedlings. Buckthorn effects on tree seedlings at younger stages (emergence and establishment) may be different because tree requirements at these stages are more related to seed size (George and Bazzaz 1999). But as the initially small seedlings grow larger, and reach small sapling size, their light requirements will likely increase to support growth (Hanson et al. 1986; Givnish 1988).

The tree seedlings were planted in a mature hybrid poplar plantation (15<sup>th</sup> growing season starting in spring 2014), which offers a very uniform environment in terms of tree stem size and systematic horizontal spacing (structure). Structural uniformity is also due

to the trees being hybrid poplar clones (genetically identical), which makes the canopy very homogenous (no effect of canopy species composition). The understory environment (light, leaf litter, soil humidity, soil nutrients) of this plantation is comparable to that of natural early-successional or partially open forests common within the region.

The study site has a recent and precisely known disturbance history. Before the establishment of the hybrid poplar plantation, the entire plantation area was an abandoned farm field dominated by herbaceous vegetation. Site preparation for planting consisted of ploughing, disking and removing all abandoned field vegetation by herbicide (glyphosate) application. Consequently, we know that the presence of glossy buckthorn individuals within the plantation dates back to less than 15 years. The open abandoned field immediately adjacent to the plantation contains large clusters of buckthorn shrubs, which are the likely source of the seeds at the origin of the individuals growing in the plantation.

### 3.2.2 Study site

The study site is a 15-year old hybrid poplar plantation located at Sainte-Catherine-de-Hatley, in southeastern Québec (Lat. N 45.27, Long. W - 72.05). This plantation is part of an experimental network of eight plantations established in 2000 on privately-owned abandoned farmland (Truax et al. 2012). Following the site preparation in fall 1999, 2 m-long rooted hybrid poplar cuttings were planted in spring 2000. Glyphosate herbicide was applied over the entire plantation area in June 2000, and between the rows in June 2001

to eliminate reappearing abandoned field vegetation (Truax et al. 2012). Since the plantation's establishment, buckthorn has naturally invaded the plantation understory.

The plantation covers approximately 0.5 ha and is entirely surrounded by a buffer row of hybrid poplars. It follows a randomized block design with 3 blocks, each including nine 12 m x 12 m main plots, randomly attributed to 9 hybrid poplar clones. Each main plot has 12 planted hybrid poplars, for an initial density of 833 stems/ha (Truax et al. 2012). Previous hybrid poplar biomass measurements required the harvesting of two trees per main plot, one per plot in 2007 and one per plot in 2012 (Figure 3.1). The canopy openings resulting from the harvesting of the two poplar trees per plot have created light conditions comparable to that of woodlots where owners have thinned the forest or where a small-scale disturbance has occurred.

The nine hybrid poplar clones have mixed parentage from the *Tacamahaca* section (*Populus maximowiczii* (abbreviation: M) native to Japan, *P. balsamifera* (abbreviation: B), native to Canada, and *P. trichocarpa* (abbreviation: T), native to the North American West Coast) and from the *Aigeiros* section (*P. deltoides* (abbreviation: D), native to Canada and the U.S., and *P. nigra* (abbreviation: N), native to Europe). Five of the nine clones, selected for their greatest differences in parentage, were used for this experiment (one letter abbreviations of parent species and clone code number): TxD-3230, DxN-3570, NxM-3729, MxB-915311 and DNxM-915508.

Each main plot selected for the experiment (5 hybrid poplar clones x 3 blocks = 15 main plots) were split in two (1<sup>st</sup> split-plot level) and a herbicide treatment was randomly attributed to one half, while the other half remained untreated (control) for a total of 30

subplots (Figure 3.1). In October 2013, double the minimal dose (7.52 kg active ingredient/ha) of glyphosate (“Round-up”) was applied to the subplots identified for the herbicide treatment. In late April 2014, the remaining dead glossy buckthorn stems were cut and removed from subplots. No soil disturbances, weeding or additional herbicide treatments were done afterwards during the whole duration of the experiment. For the control treatment halves of the split design, the natural density of glossy buckthorn was

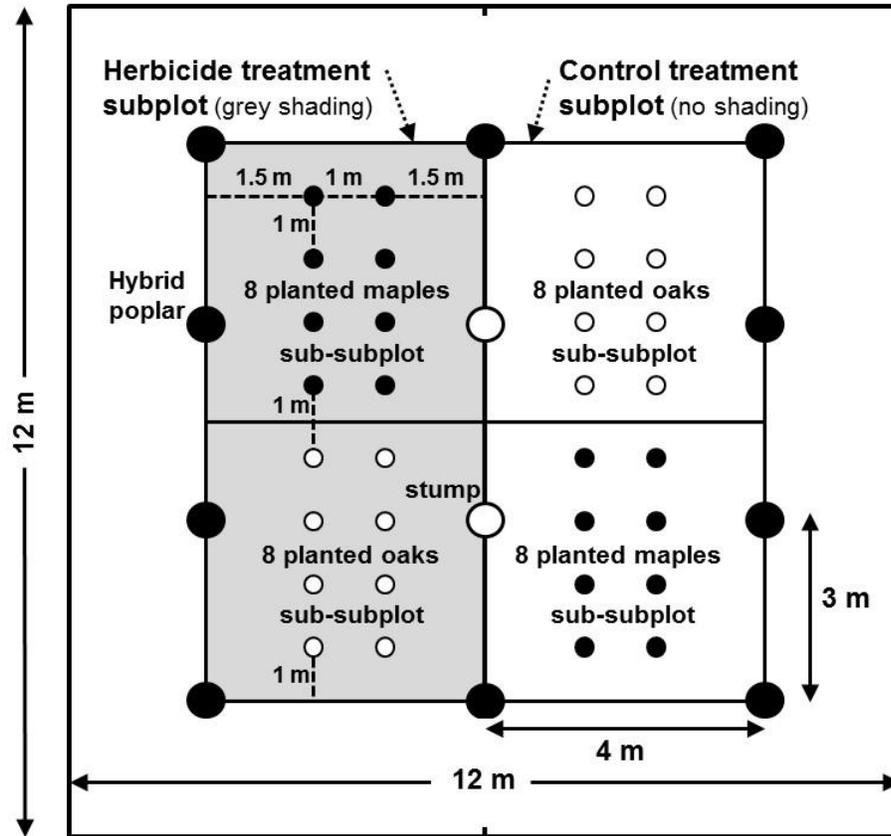


Figure 3.1 Individual hybrid poplar clone plot (12 m x 12 m, including 10 remaining hybrid poplars and 2 stumps) showing 2 treatment subplots (herbicide and control, randomly assigned left or right) and 4 planted tree sub-subplots (2 sugar maple subplots and 2 red oak subplots, randomly assigned location in each treatment) for a total of 4 experimental units per plot, and a total of 60 experimental units for the entire experimental design (4 exp. units/plot x 5 hybrid poplar clones x 3 blocks = 60)

preserved. A natural gradient in glossy buckthorn density from block 3 (glossy buckthorn at higher density, most likely first invaded through this block) to block 1 is associated to an opposite gradient of hybrid poplar biomass (resulting in greater canopy closure). In late April 2014, a 2.4 m-high (8 feet) plastic mesh fence was installed to protect the experimental design from deer browsing.

### 3.2.3 Planted tree seedlings

The tree seedlings were one year-old container-grown seedlings. Average initial height was 62 cm for sugar maple and 35 cm for red oak. They were planted on May 6 and 7, 2014, in two rows of four trees, spaced 1 m between trees on the row, and 1 m between rows (Figure 3.1). Eight tree seedlings of each species (2<sup>nd</sup> split-plot level) were planted in each sub-subplot (2 species x 2 treatments x 5 hybrid poplar clones x 3 blocks = 60 experimental units) for a total of 480 planted tree seedlings (240 per species) (Figure 3.1). This experiment follows a split-split-plot design as recommended by Petersen (1985) because the treatment (herbicide and control) and species factors are added to an existing factorial design. The height and basal diameter of each planted tree seedling were measured initially on May 12 and 13, 2014 and at the end of each of the two first growing seasons (October 2, 2014 and September 22-23, 2015). The 8 tree seedling measurements of a sub-subplot were used to calculate a mean and are considered as a single “individual” to account for variability and mortality.

### 3.2.4 Measurement of environmental and vegetation variables

#### 3.2.4.1 Light availability

Canopy openness, a proxy for light availability, was determined by the analysis of hemispherical photographs of the canopy, using the Gap Light Analyzer software v. 2.0 (Frazer et al. 1999). Two photographs were taken in each sub-subplot between July 7 and August 15, 2014: one at 1 m above the forest floor, below most of the buckthorn cover and above planted seedling height, and one at 3 m, above most of the glossy buckthorn cover.

#### 3.2.4.2 Soil nutrients and humidity

Plant Root Simulator (PRS<sup>TM</sup>-Probes) technology was used to determine soil nutrient availability, taking into account temporal variability (Western Ag Innovations Inc.). The PRS-Probes are pairs of ion-charged membranes (one for anions and one for cations) that are inserted in the soil at shallow depth for an extended period of time (40 days for this experiment) during which they exchange ions with those in the soil water (Western Ag Innovations, 2014). Three pairs of probes were inserted at 5 cm depth (from top of probe to soil surface) in each of the 60 sub-subplots from June 2 to July 11, 2014, corresponding to the peak of the growing season. Soil humidity was measured in each sub-subplot in July during a dry period (no rain 48 h prior to sampling) by conventional metal container samples for gravimetric measurements.

#### 3.2.4.3 Vegetation

The diameter at breast height (DBH) of all hybrid poplars was measured on August 15, 2014, to calculate the poplar basal area, volume and biomass per main plot, using predictive equations (stem volume, aboveground woody biomass) developed for the 13-

year old trees in the experimental hybrid poplar plantation network of Truax et al. (2014). In each sub-subplot, four 50 cm x 50 cm microplots were used to estimate the biomass of the understory vegetation. All aboveground parts of plants within these microplots were harvested and dried in ovens to produce dry biomass data.

#### 3.2.4.4 Buckthorn

To determine glossy buckthorn biomass in each sub-subplot, we used a predictive equation of aboveground biomass (Y), using basal diameter as the predictor variable (x) (allometric relationship). The predictive equation includes all aboveground biomass, including leaves, twigs and stems. Detailed methods to arrive at this predictive equation are presented in Chapter 2 (Hamelin et al. 2015). To calculate buckthorn biomass, we measured the basal diameter of all buckthorn stems taller than 50 cm in each sub-subplot. The diameter for each stem was transformed to biomass using the predictive equation and summed for each subplot. Buckthorn seedlings under 50 cm in height were counted in four 50 cm x 50 cm microplots per sub-subplot to determine their density, and were then harvested to determine total buckthorn seedling dry biomass. Total buckthorn aboveground biomass in each sub-subplot was calculated by adding total seedling dry biomass (transformed to total sub-subplot area) and buckthorn (over 50 cm in height) aboveground dry biomass (calculated using the predictive equation). To evaluate the efficacy of the herbicide treatment for controlling buckthorn over time, all buckthorn seedlings were counted after the second growing season (September 23 and 24, 2015) in one 1 m x 1 m microplot established in each herbicide treatment sub-subplot and their mean height was measured.

### 3.2.5 Statistical analyses

Tree seedling basal diameter and height increments over two growing seasons (2014 and 2015) were used as response variables for the analyses of variance (ANOVA) (measurement in fall 2015 – initial measurement in spring 2014). The model for the ANOVA includes species (2), treatments (2), hybrid poplar clone types (5), blocks (3) and their interactions. Using this same model, we tested differences in environmental and vegetation variables between species, treatments, canopy hybrid poplar clones and between blocks. We used stepwise multiple regression procedures using the R program package (R Core Team, 2014) to determine which environmental and vegetation variables explained the most variation in: 1) the amount of total aboveground biomass of buckthorn (response variable) in all plots; 2) planted seedling growth of both tree species in all plots (response variables: increment in height and diameter over two growing seasons). Prior to the analyses, a correlation matrix was done to determine if some correlation coefficients ( $r$ ) between any two factors were over 0.5 (threshold for high collinearity). When this was the case, the factor less correlated with the response variable was removed. We executed “forward” selections, using the change in the model’s  $R^2$  as the criterion to select which predictor variables to enter in the model. We evaluated the contribution of each predictor by the change in  $R^2$  and by the significance level of the ANOVA testing for the addition of the predictor.

### 3.3 Results

#### 3.3.1 Environmental and vegetation variables

Variations in environmental and vegetation variables were tested between blocks (3), hybrid poplar clone types (5), treatments (herbicide and control) and species (red oak and sugar maple). Table 3.1 shows the significance level (F and *p* values) of the differences for all measured variables. All variables associated with buckthorn abundance, soil humidity, canopy openness, understory vegetation abundance and hybrid poplar quantity showed significant differences between blocks and/or treatments (Table 3.1). No environmental or vegetation variables showed a significant difference between plots attributed to different species of tree seedlings (sub-subplots), which means that the experimental design was initially balanced and that it allows for comparisons between species. No significant differences were found for any of the soil nutrients between blocks, treatments or species. Hybrid poplar clone type canopy did not have any significant effect on any environmental or vegetation variable, or on tree seedling growth variables.

Detecting no differences in environmental variables among hybrid poplar clone type canopies is good evidence that it is highly unlikely that hybrid poplar clone type would have any effect on buckthorn. There also was no statistically significant hybrid poplar clone type effect on any buckthorn variables and on any tree seedling growth variables, nor was there a significant interaction between poplar clone type and treatment. Our third hypothesis, about the potential of hybrid poplar clone canopy influencing buckthorn or its

effect on tree seedlings, is therefore rejected. Boothroyd-Roberts et al. (2013) also did not observe any significant difference in environmental variables between hybrid poplar clone type canopies.

Table 3.1 Results from ANOVAs ( $F$  and  $p$  values) on environmental and vegetation variables of three experimental blocks, five canopy hybrid poplar clone types, two treatments (control and herbicide) and two species (sugar maple and red oak) of tree seedlings planted in the understory of a mature hybrid poplar plantation

Variable	Blocks		Poplar clone types		Treatments		Species	
	$F$	$p$ value	$F$	$p$ value	$F$	$p$ value	$F$	$p$ value
<b>Buckthorn</b>								
Stem density	3.08	0.102	0.93	0.493	29.31	< <b>0.001***</b>	0.04	0.844
Seedling density	7.42	<b>0.015*</b>	2.82	0.098	12.28	<b>0.006**</b>	0.24	0.630
Total aboveground biomass	7.58	<b>0.014*</b>	2.29	0.141	19.30	<b>0.001***</b>	0.48	0.496
<b>Soil nutrients</b>								
NO <sub>3</sub>	3.00	0.107	0.99	0.465	0.76	0.404	1.32	0.264
P	2.77	0.122	1.33	0.338	4.10	0.070	0.17	0.684
K	1.28	0.329	2.11	0.171	1.59	0.236	0.85	0.368
Ca	2.00	0.198	0.86	0.527	0.11	0.747	0.09	0.767
Mg	0.51	0.619	0.65	0.643	2.00	0.188	0.00	1.000
<b>Soil humidity</b>	5.68	<b>0.029*</b>	2.93	0.091	1.11	0.317	1.16	0.294
<b>Canopy openness</b>								
1 m	0.11	0.897	0.26	0.896	17.99	<b>0.002**</b>	0.04	0.844
3 m	1.76	0.233	0.38	0.817	10.79	<b>0.008**</b>	0.01	0.914
<b>Understory vegetation biomass</b> (without buckthorn)	1.71	0.241	0.45	0.770	29.16	< <b>0.001***</b>	0.51	0.483
<b>Hybrid poplar</b>								
Basal area	11.44	<b>0.005**</b>	3.33	0.069				
Volume	12.97	<b>0.003**</b>	2.95	0.090				
Woody biomass	13.06	<b>0.003**</b>	5.45	<b>0.020*</b>				

\* Significant at  $0.01 < p \leq 0.05$

\*\* Significant at  $0.001 < p \leq 0.01$

\*\*\* Significant at  $p \leq 0.001$

### 3.3.2 Differences between blocks

Table 3.2 shows results from the ANOVAs comparing environmental and vegetation variables between blocks (average of control and herbicide plots). Consistent with the site description (Methods, section 1.2.2), ANOVAs confirm that hybrid poplar volume and aboveground woody biomass follow a decreasing gradient from block 1 to block 3. Soil humidity also differed significantly between blocks, along an opposite gradient, increasing from block 1 to block 3. However, the observed opposite gradient of canopy openness (at 3 m) associated with the poplar biomass gradient was not confirmed by the ANOVAs.

Buckthorn seedling density and total biomass were significantly different between blocks, varying along an increasing gradient from block 1 to block 3 (Table 3.2). Buckthorns harvested for the development of the allometric relationship were up to 14 years old. This indicates that some of them invaded the plantation in 2001, one year after the site was prepared and the poplars were planted, and the same year that herbicide was applied between the poplar rows. Unlike buckthorn abundance variables, which follow a gradient opposed to that of poplar biomass (Table 3.2), the understory vegetation biomass did not vary significantly between blocks (Table 3.2).

Table 3.2 Results from ANOVAs ( $p$  values) comparing environmental and vegetation variables of the three experimental blocks in the understory of a mature hybrid poplar plantation (data are the averages of control and herbicide plots)

Variable	Unit	Block 1	Block 2	Block 3	$p$ value
<b>Buckthorn</b>					
Stem density	n/m <sup>2</sup>	1	2	4	0.102
Seedling density	n/m <sup>2</sup>	17	122	270	<b>0.015*</b>
Total aboveground biomass	g/m <sup>2</sup>	90	260	488	<b>0.014*</b>
<b>Soil humidity</b>	%	17	20	21	<b>0.029*</b>
<b>Canopy openness</b>					
1 m	%	31	32	32	0.897
3 m	%	33	33	35	0.233
<b>Understory vegetation biomass</b> (without buckthorn)	g/m <sup>2</sup>	36	20	25	0.241
<b>Hybrid poplar</b>					
Volume	m <sup>3</sup> /ha	304	199	140	<b>0.003**</b>
Woody biomass	t/ha	128	87	63	<b>0.003**</b>
Basal area	m <sup>2</sup> /ha	37	26	20	<b>0.005**</b>

\* Significant at  $0.01 < p \leq 0.05$

\*\* Significant at  $p \leq 0.01$

### 3.3.3 Differences between treatments

Table 3.3 shows the results of the ANOVAs comparing environmental and vegetation variables between treatments. Buckthorn was significantly more abundant in terms of stem density (> 50 cm in height), seedling density (< 50 cm in height) and total biomass in control treatment plots than in herbicide plots. In control plots, mean buckthorn density was 5 stems/m<sup>2</sup> and 171 seedlings/m<sup>2</sup> (Figure 3.2). In herbicide plots, buckthorns had been eliminated (0 stems/m<sup>2</sup>), but seedling density (seedlings germinated in spring 2014)

reached an average of 101 seedlings/m<sup>2</sup> during the first growing season, and an average of 114 seedlings/m<sup>2</sup> during the second growing season (Figure 3.3). Buckthorn seedlings (germinated in spring 2014) had an average height of 25 cm after two growing seasons (September 2015).

Table 3.3 Results from ANOVAs (p values) comparing environmental and vegetation variables between herbicide and control treatments in the understory of a mature hybrid poplar plantation

Variable	Unit	Herbicide	Control	Standard Error	p value
<b>Buckthorn</b>					
Stem density	stems/m <sup>2</sup>	0	5	1	< <b>0.001***</b>
Seedling density	seedlings/m <sup>2</sup>	101	171	14	<b>0.006**</b>
Total aboveground biomass	g/m <sup>2</sup>	5	554	88	<b>0.001***</b>
<b>Soil humidity</b>	%	20	19	0	0.317
<b>Canopy openness</b>					
1 m	%	33	30	1	<b>0.002**</b>
3 m	%	35	33	0	<b>0.008**</b>
(Significant poplar clone type x treatment interaction for canopy openness at 3 m, p= 0.017*)					
<b>Understory vegetation biomass (without buckthorn)</b>	g/m <sup>2</sup>	8	46	5	< <b>0.001***</b>

\* Significant at  $0.01 < p \leq 0.05$

\*\* Significant at  $0.001 < p \leq 0.01$

\*\*\* Significant at  $p \leq 0.001$



Figure 3.2 First-year seedlings of buckthorn germinated in 2014, the spring following the herbicide application, in a sugar maple herbicide sub-subplot located in block 3

Understory vegetation biomass was also significantly higher in control plots than in herbicide plots. Nonetheless, in all control plots, where buckthorn and understory vegetation are both present, buckthorn biomass was much higher than that of the understory vegetation (mean per block). The biomass of the other understory vegetation (without buckthorn) represented 31% of the total biomass of understory vegetation (understory vegetation + buckthorn) in block 1, 12% in block 2 and 6% in block 3. Overall, buckthorn biomass was higher than that of the other understory vegetation by a ratio of 12 to 1 (554 g/m<sup>2</sup> vs. 46 g/m<sup>2</sup>).

Canopy tree aboveground biomass ranged from 63 to 128 t/ha between blocks, buckthorn aboveground biomass was on average 554 g/m<sup>2</sup> (averaged over all control subplots), and the other understory vegetation aboveground biomass was on average 46 g/m<sup>2</sup> (averaged over all control plots).

At 1 m above ground level, under buckthorn cover and above planted seedling height, canopy openness was significantly lower in control plots than in herbicide plots (Figure 3.3). There was already a significant difference between treatments above most of the buckthorn cover (photographs at 3 m above ground level), but this difference is greater and more significant under most of the cover of buckthorn (photographs at 1 m above ground level). The significant interaction between poplar clone type and treatment for canopy openness at 3 m above ground (over most of buckthorn cover) appears to be a spurious effect, because treatment cannot have had any effect on the canopy above it, and it is unlikely that poplar clone type had an effect on treatment. All possible interactions between poplar clone type, treatment and species were not significant.



Figure 3.3 Hemispherical photograph of the canopy above a herbicide plot at 1 m above ground level in block 3 during the first growing season (summer 2014)



Figure 3.4 Hemispherical photograph of the canopy above a control plot at 1 m above ground level in block 3 during the first growing season (summer 2014)

### 3.3.4 Stepwise multiple regression analysis for buckthorn aboveground biomass

The environmental variables that explain a significant amount of variation in buckthorn total aboveground biomass are the canopy hybrid poplar biomass (negatively correlated), with a  $R^2$  of 0.39, followed by soil humidity (positively correlated), with an additional  $R^2$  of 0.11, and finally by log-transformed soil P flux, which adds another contribution of 0.11 to the  $R^2$ , for a total  $R^2$  of 0.61 for the analysis (Table 3.4).

Table 3.4 Results of the stepwise regression analysis between environmental variables (predictor variables) and total buckthorn aboveground biomass (response variable) for the control treatment plots in the understory of a mature hybrid poplar plantation

Environmental variables	Parameter estimate	Parameter significance ( $p$ value)	$R^2$	$\Delta R^2$	ANOVA between models	$p$ value
1. Hybrid poplar total biomass	- 0.005	< <b>0.001</b> ***	<b>0.39</b>	0.39	model 1 - model 0	< <b>0.001</b> ***
2. Soil humidity	0.048	<b>0.023</b> *	<b>0.50</b>	0.11	model 2 - model 1	<b>0.023</b> *
3. log 10 soil P	- 0.513	<b>0.011</b> *	<b>0.61</b>	0.11	model 3 - model 2	<b>0.011</b> *

\* Significant at  $0.01 < p \leq 0.05$

\*\*\* Significant at  $p \leq 0.001$

### 3.3.5 Results of the tree seedlings experiment

Of 480 tree seedlings planted in May 2014, only 6 sugar maple seedlings were dead after two growing seasons (4 in 2014 and 2 in 2015). Survival rates after two growing seasons are therefore of 100% for red oak and of 97.5% for sugar maple. Within the same

species, seedling initial size did not vary significantly between blocks, hybrid poplar clone types or treatment plots (ANOVA results not shown). The initial size of the tree seedlings was well balanced across the experimental design.

### 3.3.6 Effect of buckthorn on tree seedling growth

The mean initial height of the sugar maple seedlings (average height = 62 cm) was significantly higher than that of the red oak seedlings (average height = 35 cm) (analysis not shown). For the two following growing seasons, red oak seedlings had a higher mean height increment than sugar maple seedlings (Table 3.5), whose increment was close to zero during the second growing season (0.42 cm). Nonetheless, the initial gap between species remained highly significant after two growing seasons (data not shown). Mean initial diameter of red oak seedlings was significantly higher than that of sugar maple seedlings (data not shown). Sugar maple seedlings had a significantly higher mean diameter increment than red oak seedlings over the two first growing seasons (Table 3.5). The initial gap between species was reduced and no longer significant after two growing seasons (data not shown).

Table 3.5 Results from ANOVAs (F and *p* values) on total diameter and height increment over two growing seasons of red oak and sugar maple seedlings planted in herbicide and control treatments in the understory of a mature hybrid poplar plantation

Variable		Red oak	Sugar maple	Treatment mean	Treatment standard error	F	<i>p</i> value
Basal diameter increment (mm)	Herbicide	2.85	3.58	<b>3.21</b>	<b>0.17</b>	<b>18.96</b>	<b>0.01**</b>
	Control	1.99	2.38	<b>2.18</b>			
	Species mean	<b>2.42</b>	<b>2.98</b>				
	Species standard error	<b>0.12</b>					
	F	<b>10.51</b>					
	<i>p</i> value	<b>0.004**</b>					
Height increment (cm)	Herbicide	27.86	12.16	20.01	0.93	2.94	0.12
	Control	25.19	10.35	17.77			
	Species mean	<b>26.52</b>	<b>11.25</b>				
	Species standard error	<b>1.30</b>					
	F	<b>68.98</b>					
	<i>p</i> value	<b>&lt; 0.001***</b>					

\* Significant at  $0.01 < p \leq 0.05$

\*\* Significant at  $0.001 < p \leq 0.01$

\*\*\* Significant at  $p \leq 0.001$

Over the two first growing seasons, mean diameter and mean height increments of the tree seedlings of both species were higher in the herbicide plots than in the control plots. These results support our first hypothesis about the negative effect of buckthorn on the growth of tree seedlings. Seedling diameter increment after two growing seasons was significantly higher in the herbicide treatment. This difference increased from the first to the second growing season (data not shown). The difference between treatments in height

increment over the two growing seasons was not significant ( $p = 0.12$ ). Nonetheless, treatment means started to differentiate within a 3 cm range after two growing seasons, with the herbicide treatment showing a better mean height growth. Seedling growth did not differ between blocks and the effect of buckthorn did not differ significantly between species of tree seedlings (treatment x species interaction was not significant), therefore not supporting the hypothesis of buckthorn having a different effect on seedling species differing in shade tolerance and edaphic requirements.

### 3.3.7 Stepwise multiple regression analysis for tree seedling growth

The environmental and vegetation variables that explain a significant amount of variation in red oak basal diameter increment over two growing seasons are the amount of buckthorn biomass (negatively correlated), with a  $R^2$  of 0.32, and the amount of understory vegetation biomass (negatively correlated), which adds 0.14 to the  $R^2$ , for a total  $R^2$  of 0.46 for the explained variation of the response variable (Table 3.6). For sugar maple, the environmental and vegetation variables that explain a significant amount of the variation in its basal diameter increment are soil humidity (positively correlated), with a  $R^2$  of 0.32, followed by the amount of buckthorn biomass (negatively correlated), with an additional contribution of 0.16 to the  $R^2$ , and finally by soil K flux (positively correlated), with an additional contribution of 0.10 to the  $R^2$ , for a total  $R^2$  of 0.58 for the explained variation of the response variable (Table 6). The results of both species include buckthorn biomass, but to a different degree, supporting our second hypothesis about a different effect of buckthorn depending on the species affected. Similar stepwise multiple regression analyses were done on total height increment over two growing seasons for

each species. No environmental or vegetation variables explained a significant amount of variation in this response variable for red oak, and only soil humidity (positively correlated) could explain a significant amount of variation in total height increment for sugar maple, with a  $R^2$  of 0.26 (not shown).

Table 3.6 Results of the stepwise regression analyses between environmental variables (predictor variables) and the total diameter increment over the two first growing seasons (response variable) of red oak and sugar maple seedlings planted in both control and herbicide treatment plots in the understory of a mature hybrid poplar plantation

Species	Environmental variables	Parameter estimate	Parameter significance ( <i>p</i> -value)	$R^2$	$\Delta R^2$	ANOVA between models	<i>p</i> -value
Red oak	1. Buckthorn biomass	- 0.001	0.001***	0.32	0.32	model 1 - model 0	0.001** *
	2. Understory vegetation biomass	- 0.009	0.01**	<b>0.46</b>	0.14	model 2 - model 1	0.01**
Sugar maple	1. Soil humidity	0.197	< 0.001***	0.32	0.32	model 1 - model 0	0.001** *
	2. Buckthorn biomass	- 0.001	0.006**	0.49	0.16	model 2 - model 1	0.007**
	3. K	0.006	0.02*	<b>0.58</b>	0.10	model 3 - model 2	0.02*

\* Significant at  $0.01 < p \leq 0.05$

\*\* Significant at  $0.001 < p \leq 0.01$

\*\*\* Significant at  $p \leq 0.001$

### 3.4 Discussion

Buckthorn did reduce light availability for seedlings growing under its cover, but it did not have an effect on soil water content or soil nutrient availability. No significant

differences in edaphic conditions were observed between treatments, although the herbicide treatment resulted in the removal of an average 500 g of buckthorn dry biomass per m<sup>2</sup>. This result supports the description of glossy buckthorn as a species with low edaphic requirements, which does not require large amounts of water or soil nutrients, and which can therefore prosper over a very wide range of conditions and ecosystems (Mills et al. 2012). Light availability is the only environmental variable for which a significant difference was observed between control and herbicide treatments. A reduction in light availability by buckthorn had already been suggested before as buckthorn's main negative effect on native plant environment (Frappier et al. 2003). To our knowledge, it is the first time that it is experimentally measured and detected as statistically significant. This result suggests that species with different light requirements could be affected to a different degree by buckthorn. However, in our experiment, the ANOVA did not have a significant treatment x species interaction, indicating that the shade produced by buckthorn did not generate a significantly different growth response in the seedlings of the two species. Yet, the planted seedlings were still relatively small after two growing seasons (average height 73 cm for sugar maple and 62 cm for red oak), and a different growth response of sugar maple and red oak under buckthorn shade may appear after several more years of growth.

In our experimental design, some support for a different reaction to buckthorn by the seedlings of the two tree species comes from the results of the multiple regression analyses. Different environmental and vegetation variables explain the variation in diameter growth of each of the two species tested, but both species have one variable in common, and that is the total aboveground biomass of buckthorn ( $R^2 = 0.32$  for red oak,

$R^2 = 0.16$  for sugar maple). Aboveground biomass of buckthorn and other understory vegetation were the only two significant variables explaining variation in diameter growth for red oak. This result is consistent with the intermediate tolerance to shade of this species (Humbert et al. 2007), which would make it more sensitive to shading by buckthorn. In contrast, two out of three significant variables explaining sugar maple diameter growth were edaphic variables (soil humidity and soil K). This is consistent with the high edaphic requirements of this species (Park and Yanai 2009). This differential effect of buckthorn on the diameter growth of seedlings of tree species based on their tolerance to shade supports the observations of some authors of shifts in composition towards shade-tolerant species under buckthorn cover (Frappier et al. 2003; Fagan and Peart 2004). This species-specific effect on the seedlings could be compared to a “filter” through which not all tree species will equally grow and survive. George and Bazzaz (1999) described a “filter” effect produced by the fern understory stratum in New England deciduous forests, and they explained how it could lead to an altered canopy tree composition and to modifications in species distribution. Buckthorn could be creating a similar effect when it is abundant in the forest understory.

Our observations of a species tolerant to shade and a species of intermediate tolerance to shade being both affected in their growth by buckthorn possibly forecasts a generalized delay in the canopy replacement, as suggested by Fagan and Peart (2004). Buckthorn (total aboveground biomass) was the second most important variable explaining the variation in sugar maple diameter growth, which indicates that even species that are tolerant to shade can be affected by buckthorn abundance. Management practices preventing buckthorn from reaching an abundance at which it affects tree seedlings, of

any level of shade tolerance, need to be implemented, whatever species the regeneration is composed of, to avoid losses in forest production and important changes in forest species composition and distribution.

Our data contribute to narrowing down the range of buckthorn density that includes the density threshold under which buckthorn has no significant negative effect on tree seedlings. In the control plots, buckthorn stem densities ranged between 3 to 7 stems/m<sup>2</sup> (average for block 1 and 3, respectively), which is within the range where could lie the threshold under which buckthorn does not have a significant negative effect on tree seedling density. This interpretation is supported by the results of Owen Koning and Singleton (2013), who examined the effect of buckthorn at densities averaging 1 stem/m<sup>2</sup> and did not find a significant effect on tree seedling density. Their study also included one stand invaded by buckthorn at a higher density of 8 stems/m<sup>2</sup>, where a significant negative effect of buckthorn was observed. Owen Koning and Singleton (2013) proposed to manage invasive species by reducing their abundance below a certain threshold where the negative effects on native species are not significant, rather than trying to eradicate the species from an area, which is almost always impossible. The threshold under which buckthorn has no significant effects on tree seedlings has not been identified in our experiment, but the range can be narrowed down to buckthorn densities between 1 and 3 stems/m<sup>2</sup>.

The very high buckthorn seedling densities under the buckthorn cover (171 seedlings/m<sup>2</sup> on average in control plots) and in herbicide-treated plots (101 seedlings/m<sup>2</sup> on average), and the rapid growth rate of these seedlings (25 cm-high two growing seasons after germination), challenges the idea that native tree seedlings will be

able to germinate, establish and be recruited in the stand. Planting tree seedlings to regenerate logged areas (clear cut or shelterwood cut) or understories of low density forests (ex. early successional intolerant hardwood stands) may be essential to ensure a well-stocked future stand. Follow-up measurements in our experimental design will provide information on whether a single herbicide treatment was enough to ensure the further development of the planted seedlings and their recruitment as saplings.

Sites that appear to be most at risk of invasion by buckthorn are probably those with higher canopy openness and higher soil water content, whatever their soil fertility status. In their analysis, Frappier et al. (2003) found that buckthorn basal area was only correlated with canopy openness. In our study plantation, the variation in the total amount of buckthorn aboveground biomass was explained by the canopy hybrid poplar biomass (negatively correlated; proxy for canopy closure) and soil humidity (positively correlated), two variables correlated together at 0.48. The poplar biomass being correlated to canopy openness at 3 m (correlated at 0.43), these results are consistent with observations made in many different forest types of the region, where buckthorn was noted to be particularly abundant in forests with partly open canopies and with moderately well to imperfectly drained soils (Benoit Truax, personal observation). Other authors have pointed out that buckthorn grows well on poorly drained sites and that its abundance is linked to canopy openness (Godwin 1943; Converse 1984; Catling and Porebski 1994; Sanford et al. 2003; Nagel et al. 2008; Lee and Thompson 2012). Soil P also had a significant input in the analysis and this variable was associated with hybrid poplar yield in a previous study including the study plantation and 7 other hybrid poplar plantations (Truax et al. 2012). Prior to the establishment of the hybrid poplar plantation

used in our study, a fertility gradient was recorded from block 1 to 3 (soil P concentration: block 1, 110.4 kg/ha; block 2, 26.8 kg/ha; block 3, 14 kg/ha) and there was no gradient in soil humidity. Fifteen growing seasons later, the aboveground hybrid poplar biomass follows the initial gradient in soil fertility and has created a weak, but significant opposite gradient in soil humidity. Hybrid poplars are known to have high soil water and nutrient uptakes (Vance et al. 2014; Fortier et al. 2015). Nutrients being stocked in the poplar biomass, the nutrient gradient in the plantation is no longer significant after 15 growing seasons, but P concentration is the only nutrient that still follows a decreasing trend from block 1 to 3. P thus seems to be an artefact from the initial fertility gradient and it is still correlated to hybrid poplar biomass (0.36). It is thus consistent with field observations and with the literature, that buckthorn is more abundant in block 3 where light and water are more available and where P is less available (negatively correlated).

The results of this study on the effects of buckthorn on tree seedlings are likely to be generally applicable to early successional, partially open, hardwood forests (dominated mostly by intolerant hardwoods (poplars, birches, ashes, etc.)) that occur throughout southeastern Canada and the northeastern United States (Northern Hardwoods forest). This is because the understory environment of the 15-year old hybrid poplar plantation used for the experimental design has many environmental factors that are very similar to those of naturally regenerated forests of several decades in age (Boothroyd-Roberts et al. 2013b). Indeed, Boothroyd-Roberts et al. (2013b) found that 10-year old productive hybrid poplar plantations already had similar basal area, canopy closure and leaf litter accumulation, to that of nearby young second growth woodlots (ranging from 31 to 58

years in age). The plantation used in the present study (Ste-Catherine) was also one of the 8 hybrid poplar plantations that were compared to adjacent abandoned fields and nearby second growth woodlots by Boothroyd-Roberts et al. (2013b).

### 3.5 Conclusion

This experiment allowed us to measure a reduction in light availability for tree seedlings, which was suggested in the literature, but never measured before. A reduction in seedling growth under a cover of buckthorn was measured for the two species tested, and our analyses showed that buckthorn has a significant input in explaining tree seedling growth for both species, reinforcing the idea that it is the presence of buckthorn that affects the seedlings. Moreover, this experiment gives indications of a differential effect of buckthorn on tree seedlings growth for species with different light requirements. Other authors had related buckthorn's presence with shifts in dominance towards species that are tolerant to shade, and this experiment resulted in a positive answer for this hypothesis. Finally, this experimental manipulation took place in Canada, where no research on the effect of buckthorn on tree seedling is available, and more precisely in a hybrid poplar plantation that has understory conditions comparable to those of early successional forests with partially open canopies. It is the first time that a forest environment similar to early successional forests, common throughout the Northern Hardwood forest region, is used for studying buckthorn. Finally, using nursery-produced seedlings in this experiment provides valuable information on how buckthorn can affect reforestation and under-planting projects.

Our short-term results on buckthorn seedling density and growth rate, and on the negative effect of buckthorn on native tree seedling growth provide support for the rapid reforestation of sites that have been recently cleared and treated with herbicide, and more generally of sites that have a partially open canopy and moderately well to imperfectly drained soils. Relying on natural regeneration in these situations may be ill advised, especially in the highly fragmented landscapes typical of southeastern Canada, where remaining surrounding forested areas, upon which colonization success by native trees depends for seed sources, are often distant. Reforesting (after agricultural abandonment or clear cutting) or under-planting (in appropriate early successional stands or mature poplar plantations) appear to be necessary in order to outpace buckthorn colonization.

Our conclusion is that shading by buckthorn is what produces the negative effect on tree seedling growth. Therefore, although shade-tolerant species, such as sugar maple, may be able to grow in the presence of buckthorn, albeit poorly, other species with higher light requirements, such as red oak or white ash, may have large growth reductions and have great difficulty passing through the buckthorn filter. Sugar maple is very rarely planted because it is abundant in naturally regenerated forests. Red oak, however, is a species of choice for under-planting and for plantations. Our results therefore have important implications for the restoration of red oak under partial tree cover if buckthorn has invaded the understory. Restoration of valuable hardwood species by under-planting in young low-density early successional forests or plantations on abandoned farmland are currently promoted by forest managers in Québec, but it may prove mostly unsuccessful if no special management practices are developed to control this invasive introduced species.

## **CHAPTER FOUR: The effect of glossy buckthorn on planted forest herbs**

### 4.1 Introduction

Exotic species represent between a quarter and a third of the plant species of the eastern Canadian provinces and American states (Lavoie et al. 2012). While most of them integrate into native ecosystems without producing major changes (Stohlgren et al. 2006; Mills et al. 2009), a small number of exotic plants, called invasive species, can impair native ecosystems and result in serious ecological and economic consequences (Gordon 1998; Mack et al. 2000; Webster et al. 2006). However, the abundance of an exotic species has been shown to not be indicative of its impact on native species (Ricciardi and Cohen 2007). Furthermore, a species can be a driver of change in its new environment, but it can also only be a “passenger” taking advantage of the current state of an ecosystem, such as for example a “disturbed” state (Macdougall and Turkington 2005). In the latter case, control efforts would not be justified because the opportunistic species is not the primary source of the negative effects and its eradication will probably not restore the altered ecosystem. In addition, control efforts themselves risk resulting in negative impacts on native species or even foster new invasions by other species (Westman 1990). Resources for control being limited and control actions being expensive, labor-intensive and implying long term commitments, prioritization of the exotic species requiring control is essential. Therefore, it is necessary to experimentally test the effects of exotic plants to verify causal links between the effects observed and their presence and abundance, and then prioritize the monitoring and control of species for which a causal link has been established (Macdonald et al. 1989).

One species of concern is glossy buckthorn (*Frangula alnus* Miller, syn. *Rhamnus frangula*), an exotic shrub introduced for ornamental purposes that is now naturalized throughout Eastern North America and dominant in several ecosystems. It is particularly abundant on sites with humid and acid soil conditions, and light availability seems to be a limiting factor (Godwin 1943; Converse 1984; Catling and Porebski 1994; Sanford et al. 2003; Lee and Thompson 2012). Nonetheless, buckthorn can also thrive under a wide range of edaphic, light, forest and climatic conditions (Godwin 1936; Godwin 1943; Sanford et al. 2003; Schoeb et al. 2012; Mills et al. 2012). Its invasion success seems to be mainly due to its low ecological requirements, a prolific seed production, excellent dispersal and high germination, recruitment and growth rates (Mills et al. 2012). It causes serious concerns among forest managers and conservationists because its spread is facilitated by openings in the forest canopy (Burnham and Lee 2010; Lee and Thompson 2012); such as in small natural gaps and in gaps created by partial cutting. Buckthorn is very efficient at outcompeting native species in the colonization of canopy gaps, where it tends to form a very dense pure cover, limiting light availability to the forest floor (Converse 1984; Frappier et al. 2004; Nagel et al. 2008). Following an invasion, native tree species composition can be shifted towards shade-tolerant species and forest succession can be delayed or stopped, reducing the economic value, productivity and diversity of a forest stand (Possessky et al. 2000; Fagan and Peart 2004).

While most studies examining the effect of buckthorn focussed on the response of native tree seedlings, only a few have included herbaceous forest plants, or forest herbs. Mason et al. (2009) observed that the effect of woody invasive species is generally stronger on herbaceous plants than on other plant forms. The study of this stratum could

thus provide a more accurate and comprehensive assessment of the effect of buckthorn on the entire forest understory. From a conservation perspective, because buckthorn is capable of invading humid and low-nutrient sites, where a large number of endangered plant species also occur (Catling and Porebski 1994), information on the effect of buckthorn on forest herbs will allow a better prediction and prevention of the potential damages to the ecosystem. Forest herbs are also planted for restoration purposes (Mason et al. 2009) and some species are cultivated as non-timber forest products. Both activities often take place in disturbed or managed forests or plantation understories (Boothroyd-Roberts et al. 2013a), where buckthorn may be especially likely to invade. Increased knowledge of the effects of buckthorn on forest herbs will help include glossy buckthorn in management, restoration or cultivation plans in order to preserve ecological and economic benefits.

In several New Hampshire pine-mixed hardwood forests and plantations, high basal areas of glossy buckthorn have been associated with lower herbaceous plant cover and lower ground level plant species richness (Frappier et al. 2003). In contrast, no effect of buckthorn removal on herb cover and herb species richness was detected in two experimental manipulations done in the same region and forest types, one of them testing results five years after buckthorn removal (Frappier et al. 2004; Owen Koning and Singleton 2013). The authors of these last studies respectively nuanced the absence of a causal link because of high variability intrinsic to the sites and by the low densities of buckthorn, preventing the detection of a significant effect. Indeed, Owen Koning and Singleton (2013) observed a significant negative effect on red maple seedling density and overall woody plant stem density only in the forest type where buckthorn was very much

more abundant than in the other forest types studied. They described a threshold beyond which buckthorn may have a significant detrimental effect and estimated that it should lie between 1.5 and 8.25 stems of buckthorn per square meter. Sinclair and Catling (1999) have observed an increase in native plant species cover after removal of buckthorn in the forests of Southern Ontario. In Northern Allegheny Plateau riparian savannas in Pennsylvania, Possessky et al. (2000) observed a reduced percent herb cover in plots invaded by buckthorn compared to control savanna plots, a change in species dominance toward shade-tolerant species, but no effect on herb species richness. A causal link between glossy buckthorn and performance of forest herbs has thus not yet been clearly established. Moreover, a change in dominance toward shade-tolerant species, and the reduction in understory species richness observed by Frappier et al. (2003) suggest that different species of plants may be differently affected by buckthorn. Knowing more about differences in susceptibility to buckthorn among herb species would help conservationists identify species that are more at risk and guide the choice of less sensitive species to be transplanted in restoration projects.

Glossy buckthorn is considered one of the most serious invaders in Eastern North America by the Canadian and United States governments. Control actions aiming to reduce its abundance or to eradicate it have taken place in both countries, but very little research has been done in Canada. Several authors have emphasized the importance of doing regional studies to evaluate the effects of invasive species (Frappier et al. 2004; Ricciardi and Cohen 2007; Nagel et al. 2008). The response to buckthorn invasion may vary depending on the ecosystem and the geographical location (Westman 1990; Frappier et al. 2004; Ricciardi and Cohen 2007; Nagel et al. 2008). Research on buckthorn has

been mostly conducted in New England pine-mixed forests, and little information is available on buckthorn effects in other ecosystems. Some forest types have been shown to be more susceptible than others to invasion by buckthorn (Owen Koning and Singleton 2013) and the composition of a forest in terms of canopy trees may influence the effect of buckthorn on the forest understory. In southern Québec, early successional, partially open hardwood forests are more likely to be invaded by buckthorn, but there has been no research on how buckthorn affects ecosystems in that region and that forest type. This type of forest covers a vast area in the region, where human settlements and agriculture activities have highly fragmented the landscape and modified ecosystems. Radical control actions have also faced social disapproval in the past years because of their adverse effect on landscape aesthetics (Le Haut-Saint-François 2014). Examining the effect of buckthorn in early successional, partially open hardwood forests in southern Québec (Canada) would much contribute much to the question of whether the control of buckthorn is necessary.

The objectives of this study are to test in a field experiment if the exotic shrub glossy buckthorn has a negative effect on the survival and growth of understory forest herbs, and if so, to determine how this effect varies depending on the particular herb species and the overhead tree canopy type. This experiment was done in parallel to a similar experiment we conducted on transplanted tree seedlings (Chapter 3). Three herb species were planted in May 2014 in the understory of a 15 year-old experimental hybrid poplar plantation, under two types of hybrid poplar clones. In fall 2013, a herbicide treatment was applied to half of the plots, and in spring 2014, prior to transplanting herbs, all remaining stems of buckthorn were cut to obtain a complete initial buckthorn removal treatment. In this

experimental design, as many factors as possible were controlled (canopy composition and structure, age of the herb transplants, deer browsing exclusion) and as many environmental factors as possible were quantified (light availability, soil properties, canopy hybrid poplar biomass, understory vegetation biomass, buckthorn density and biomass) in order to measure their effects on three species of forest herbs, and their possible interactions with the effects of glossy buckthorn.

The advantages of using a plantation for this experiment are the uniformity of the tree stem sizes and distribution (structure), especially because the trees are hybrid poplar clones (genetically identical individuals), as well as the uniform nature of the canopy (no effect of canopy species composition and minimal differences within a clone type). In addition, because reforestation of abandoned farmland and restoration of forest understories are becoming more widespread, the results of this study will be useful for answering a number of questions, of fundamental and applied nature. Furthermore, the understory of the studied poplar plantation can be compared to that of natural early-successional forests that cover a considerable area within the region.

## 4.2 Methods

### 4.2.1 Study site

The study site is a 15 year-old hybrid poplar plantation located in Sainte-Catherine-de-Hatley, in southeastern Québec (Lat. N 45.27; Long. W -72.05). In the past, the site was used for cultivation or pasture (Boothroyd-Roberts et al. 2013b). Herbaceous vegetation typical of abandoned fields was dominant on the site prior to plantation establishment

(Truax et al. 2012). This plantation is part of an experimental network of eight plantations established in 2000 on privately-owned abandoned farmland (Truax et al. 2012). In fall 1999, the site was prepared for planting by ploughing, disking and by the removal of the early-successional vegetation. In spring 2000, 2 m-long rooted hybrid poplar cuttings were planted to 30-40 cm depth. Glyphosate herbicide was applied over the entire plantation area in June 2000, and between the tree rows in June 2001 to eliminate reappearing abandoned field vegetation (Truax et al. 2012).

#### 4.2.2 Experimental hybrid poplar plantation

As for all the plantations of the experimental network, the Sainte-Catherine-de-Hatley plantation follows a randomized block design, with 3 blocks and 9 hybrid poplar clones. The plantation is surrounded by a buffer row of hybrid poplars. Each block includes nine 12 m x 12 m main plots, randomly attributed to 9 different hybrid poplar clones. Each main plot has 12 planted hybrid poplars, planted in 3 rows of 4 trees (spaced 3 m apart on the row, with rows 4 m apart) for an initial density of 833 stems/ha (Truax et al. 2012). Two of the nine clones were selected for this experiment for their greatest differences in parentage. These are the DxN-3333 clone (hybrid of two species from the *Aigeiros* section of the *Populus* genus: *P. deltoides* (abbreviation: D), native to Canada, and *P. nigra* (abbreviation: N), from Europe) and the MxB-915303 clone (hybrid of two species from the *Tacamahaca* section of the *Populus* genus: *P. maximowiczii* (abbreviation: M), from Japan, and *P. balsamifera* (abbreviation: B), native to Canada). These two clones have dissimilar ecology, yield, physiology, structure and biomass

allocation (stem, branches and roots) which maybe influence the light availability and possibly the available soil nutrients after 15 growing seasons.

Each main plot selected for the experiments (3 blocks x 2 clones = 6 main plots) were split in two (1<sup>st</sup> split-plot level) and a herbicide treatment was randomly attributed to one half, while the other half remained untreated (control) for a total of 12 subplots. In October 2013, double the minimal dose of glyphosate (“Round-up”, from Monsanto) was applied with a backpack sprayer to the herbicide subplots (6 subplots of 6 m x 12 m). In late April 2014, the remaining dead glossy buckthorn stems were cut and removed from plots. No soil disturbance, weeding or additional herbicide treatment were done afterwards during the whole duration of the experiment. This will enable us to do future follow up measurements of the efficiency of the herbicide treatment, which is considered to be reproducible at a larger scale, if it is proven to be efficient in controlling buckthorn. In the control treatment halves of the split design, no control of glossy buckthorn was done, preserving the natural density of glossy buckthorn in control subplots. A natural gradient in glossy buckthorn density from block 3 (glossy buckthorn at higher density, most likely first invaded through this block) to block 1 is associated to an opposite gradient of hybrid poplar yield (canopy closure), generated by an initial decreasing gradient in soil fertility from block 1 to 3 at the time of plantation establishment.

In late April 2014, an 8 foot-high plastic mesh fence was installed to protect the study site from deer browsing. Excluding this effect from the experiment was justified by a previous study (Truax et al. 2012) where deer browsing at the Sainte-Catherine site had been measured at 60% of poplar seedlings browsed. Without the exclusion of deer, the

probability is high that the potential effects of glossy buckthorn on understory herbaceous plants would have been confounded with deer browsing effects on planted forest herbs.

#### 4.2.3 Transplantation of forest herbaceous plants

Three understory herbaceous species were planted in this experimental design: blood-root (*Sanguinaria canadensis* L.), wild ginger (*Asarum canadense* L.) and Solomon's seal (*Polygonatum pubescens* (Willd.) Pursh.). Wild ginger and blood-root transplants were studied previously in the same hybrid poplar plantation network and both showed good potential for cultivation or conservation in plantation understories (Boothroyd-Roberts et al. 2013a). Both wild ginger (food and medicinal uses) and blood-root (medicinal uses) are known non-timber forest products (NTFPs). However, there is considerable evidence that forest understory herbs cannot withstand any harvesting because of slow population growth, and especially those species that are sought for their bulbs/roots, thus killing the harvested plants (Nantel *et al.*, 1996). In Québec, blood-root and wild ginger are legally designated as “vulnerable” because they were potential targets of harvesting to supply nurseries in native shade garden plants (MDEL 2014). Blood-root, wild ginger and Solomon's seal are all species typical of Southern Québec's rich hardwood forest understories.

The use of mature herbaceous plants can better reflect the effect of glossy buckthorn than a response measured at earlier growth stages (i.e. seedlings), where environmental variables can have more important incidence on the growth of plants (Primack 2010). Using transplants also allows us to measure the response to buckthorn directly on individual plants, which is a more sensitive measurement than overall understory herb

cover. In addition, the transplants more accurately represent a restoration or cultivation reality. The transplants used were container-grown and were planted between May 8 and 9, 2014. They were not all of a similar size initially. Therefore, a screening based on plant size was done previous to plantation so that the distribution of plants differing in sizes was as homogeneous as possible among subplots, plots and blocks. Once the expansion of leaves and above ground structures had been fully attained, initial size measurements were taken on all plantlets of each species (between May 27 and June 13, 2014) to establish initial size and to verify the uniform distribution of the plant sizes among plots.

This experimental design corresponds to a split-split-plot design, as described by Petersen (1985). 20 plantlets of each of the three species (2<sup>nd</sup> split-plot level) were planted in 12 subplots, for a total of 36 experimental units (sub-subplots: 3 blocks x 2 clones x 2 treatments x 3 species) and 720 plantlets (240 per species). The plantlets were planted in two rows of 10 individuals with a spacing of 30 cm between the plants on the row and 20 cm between rows (40 cm between rows of different species). Two rows for a species form a rectangular unit of 2 m x 0.75 m, and three units (one for each species) were placed side by side in a random order in each of the 12 subplots.

The central area (including plantation area) of the main plots were amended with lime (calcium hydroxide) in October 2013, in order to increase the soil pH and improve soil conditions for calcicolous herbaceous plants (Boothroyd-Roberts et al. 2013a). An amount of 166 g of lime per m<sup>2</sup> was added to the entire area (2 kg for 12 m<sup>2</sup>) of each main plot.

#### 4.2.4 Measurements of transplanted forest herbs

Relative growth rate (RGR) for individual plants of each species, based on percent biomass gain, was used in the analyses as the variable describing growth for all three species. Relative growth rates were calculated using the following formula from Hunt (1990):  $RGR = (\ln W_2 - \ln W_1) / (t_2 - t_1)$ , and were expressed in g/g/year. Initial measurements (Time 1), taken shortly after planting (June 2014), after full plant stem and leaf development, and measurements taken one year later (Time 2, June 15-19, 2015) were used to calculate relative growth rates (RGR) for each experimental unit. Data at time 1 (May 27-June 13, 2014) represent growth produced from the resources stocked in the rhizomes of the plants during the previous growing season, that is to say the last one spent in the nursery. Data taken at time 2 (June 2015) represent growth from resources stocked after transplantation, during the plant's first growing season in the plantation understory (the spring and summer 2014 growing season), either under a control (with buckthorn) or a herbicide (no buckthorn) treatment. The duration of this study being limited by the normal duration of the M.Sc. program (2 years), only one growing season-response to glossy buckthorn was measured for the herbaceous plants, which was in spring 2015. However, for publication purposes, a second set of measurements will be made in June 2016 (2 full growing seasons after transplantation).

To calculate plant biomass using non-destructive measurements of leaves and aboveground structures, predictive equations of total dry biomass ( $Y$ ) were built for each forest herb species using specific size measurements as predictor variables ( $x$ ). After initial size measurements were made in 2014, a subsample of 12 plants per species was harvested to determine aboveground, belowground and total biomass. All collected

samples were dried in a drying oven to determine dry mass. Plant size measurements depended on the individual morphology and growth pattern of each species, and the size measurements that were the best predictors of dry biomass were determined by regression analyses (single variable regression). Regression model selection was based on the Akaike Information Criterion (AIC) and on the fit of the model ( $R^2$ ). The selected regression models are all power functions.

Survival was assessed while measuring the plants, at Time 1 and Time 2 (June 2014 and June 2015), by recording the number of live plants. Survival per experimental unit in 2015 was used as a response variable in an ANOVA testing differences between blocks, clone types, treatments and species. There was a very low post-transplantation mortality observed in June 2014 (4% for *S. canadensis*, 2% for *A. canadense*, and none for *P. pubescens*; not shown). The few individuals that died soon after planting were probably weaker plants, injured plants or the result of transplantation shock. In order to remove this “transplantation” effect from the survival data, the number of dead individuals in June 2014 was not considered in the calculation of survival rates of June 2015.

#### 4.2.5 Measurement of environmental variables

As for the experiment on tree seedlings presented in chapter 3, light availability, soil humidity, soil nutrient availability, buckthorn stem and seedling density, buckthorn biomass, understory vegetation biomass and canopy poplar biomass were measured.

One photograph at each height (1 and 3 m above ground level) was taken per treatment plot, four sets of PRS probes were buried in each of the 12 treatment plots, a

sample to measure soil humidity was collected in each treatment plot, four 50 cm x 50 cm microplots were used to estimate the biomass of the understory vegetation in each treatment plot and in each treatment plot, all of the glossy buckthorn stems were counted and their basal diameters were measured for subsequent conversion into biomass values. Buckthorn seedlings were counted in the four 50 cm x 50 cm microplots used for understory vegetation biomass measurement. Hybrid poplars included in the plot were measured for conversion in aboveground biomass.

## 4.3 Results

### 4.3.1 Environmental and vegetation variables

Variations in environmental and vegetation variables were tested between blocks (3), clone-types (DxN-3333 and MxB-915303) and treatments (herbicide and control) to characterize the forest herb growing conditions under these factors. Table 4.1 shows the significance level (F and *p* values) of the differences for all measured variables.

Buckthorn stem density and total aboveground biomass, canopy openness at 1 m above ground level and understory vegetation biomass showed significant differences between blocks and/or treatments (Table 4.1). Clone-type canopy only had a significant effect ( $p < 0.05$ ) on canopy openness at 1 m above ground level, under most of the buckthorn cover. No significant differences were found for any of the soil nutrients, for soil humidity, or for hybrid poplar variables between blocks, clone types or treatments ( $p > 0.05$ ).

Table 4.1 Results from ANOVAs ( $F$  and  $p$  values) comparing environmental and vegetation variables of three experimental blocks, two canopy hybrid poplar clone types (DxN-3333 and MxB-915303) and two treatments (herbicide and control) of a mature hybrid poplar plantation.

Variable	Blocks		Clone types		Treatments	
	$F$	$p$ value	$F$	$p$ value	$F$	$p$ value
<b>Buckthorn</b>						
Stem density	54.76	0.0179*	0.93	0.437	31.68	< 0.001***
Seedling density	2.65	0.274	0.38	0.600	1.46	0.294
Total aboveground biomass	11.49	0.080	1.91	0.301	9.64	0.0361*
<b>Soil nutrients</b>						
NO <sub>3</sub>	0.21	0.826	1.67	0.325	0.00	0.978
P	0.61	0.621	0.67	0.500	0.57	0.493
K	0.91	0.523	1.35	0.365	0.62	0.475
Ca	3.04	0.248	0.37	0.607	0.02	0.905
Mg	1.01	0.498	0.46	0.566	1.45	0.295
<b>Soil humidity</b>	0.65	0.607	1.49	0.347	0.24	0.651
<b>Canopy openness</b>						
1 m aboveground	30.37	0.0319*	26.05	0.0363*	0.35	0.584
3 m aboveground	9.18	0.098	1.09	0.405	0.72	0.445
<b>Understory vegetation biomass (without buckthorn)</b>	0.05	0.956	0.51	0.549	16.5	0.0154*
<b>Hybrid poplar</b>						
Volume	5.65	0.150	3.17	0.217		
Biomass	5.32	0.158	7.89	0.107		

\*\*\* Significant at  $p < 0.001$

\* Significant at  $p < 0.05$

#### 4.3.1.1 Differences between blocks

Table 4.2 shows results from the ANOVAs comparing environmental and vegetation variables between blocks.

Table 4.2 Results from ANOVAs ( $p$  values) comparing environmental and vegetation variables of the three experimental blocks in the understory of a mature hybrid poplar plantation (data are the averages of control and herbicide plots)

Variable	Unit	Block 1	Block 2	Block 3	Standard Error	$p$ value
<b>Buckthorn</b>						
Stem density	stems/m <sup>2</sup>	1	2	3	0	0.0179*
Seedling density	seedlings/m <sup>2</sup>	25	29	236	74	0.274
Total aboveground biomass	g/m <sup>2</sup>	185	105	469	56	0.080
<b>Soil humidity</b>	%	19	22	20	2	0.607
<b>Canopy openness</b>						
1 m aboveground	%	29	35	30	1	0.0319*
3 m aboveground	%	30	35	34	2	0.196
<b>Understory vegetation biomass (without buckthorn)</b>	g/m <sup>2</sup>	34	41	35	18	0.956
<b>Hybrid poplar</b>						
Volume	m <sup>3</sup> /ha	228	192	90	434	0.150
Biomass	kg/m <sup>2</sup>	9	8	4	1	0.080

\* Significant at  $p < 0.05$

Consistent with the site description (Methods, section 4.2.2), mean hybrid poplar volume and aboveground woody biomass follow a decreasing gradient from block 1 to block 3. Differences in poplar variables between blocks were not significant in this experiment (Table 4.2) likely because of the low number of replicates, contrasting with the significant differences observed in a larger experimental design including five clone types from the same plantation (Chapter 3, Table 3.2). Associated with the hybrid poplar gradient, canopy openness at 3 m above ground level (over most of buckthorn cover) was lower in block 1 than in block 2 and 3, but this relationship was not significant. Consistent with these gradients, buckthorn stem density (stems > 50 cm in height) was significantly different between blocks, varying along an increasing gradient from block 1 to block 3 (Table 4.2).

Canopy openness at 1 m above ground level (underneath most of buckthorn cover) was significantly different between blocks (block 2 having the most open canopy, where buckthorn total biomass was the lowest), but did not vary along a particular gradient (Table 4.2). Humidity and biomass of understory vegetation did not vary significantly between blocks and did not follow a particular gradient between blocks (Table 4.2).

#### 4.3.1.2 Differences between treatments

Table 4.3 shows the results of the ANOVAs comparing environmental and vegetation variables between treatments.

Not surprisingly, buckthorn was significantly more abundant in terms of stem density (stems > 50 cm in height) and total biomass in control treatment plots than in herbicide

plots. In control plots, mean buckthorn density was 4 stems/m<sup>2</sup> and 127 seedlings/m<sup>2</sup>. In herbicide plots, buckthorns had been cut and removed (0 stems/m<sup>2</sup>), but seedling density (seedlings of the year, that germinated in spring 2014 from seeds produced in 2013) reached an average of 66 seedlings/m<sup>2</sup>.

Table 4.3 Results from ANOVAs (*p* values) comparing environmental and vegetation variables between herbicide and control treatments in the understory of a mature hybrid poplar plantation

Variable	Unit	Herbicide	Control	Standard Error	<i>p</i> value
<b>Buckthorn</b>					
Stem density	stems/m <sup>2</sup>	0	4	1	0.0049**
Seedling density	seedlings/m <sup>2</sup>	66	127	36	0.294
Total aboveground biomass	g/m <sup>2</sup>	2	503	114	0.0361*
<b>Soil humidity</b>					
	%	20	20	1	0.651
<b>Canopy openness</b>					
1 m aboveground	%	31	32	1	0.584
<b>Understory vegetation biomass (without buckthorn)</b>					
	g/m <sup>2</sup>	6	68	11	0.0154*

\* Significant at  $p < 0.05$

\*\* Significant at  $p < 0.01$

Understory vegetation biomass was also significantly higher in control plots than in herbicide plots. Nonetheless, in all control plots, where buckthorn and understory vegetation are both present, buckthorn biomass was higher than that of the understory vegetation (mean per block). The biomass of the understory vegetation represented 24% of the total biomass of understory vegetation biomass (understory vegetation + buckthorn) in block 1, 7% in block 2 and 4% in bloc 3.

No differences in canopy openness or soil humidity conditions between treatments were significant. All possible interactions between clone-types, treatments and species were not significant ( $p > 0.05$ ).

#### 4.3.2 Forest herbs allometric relationships

Three outliers were removed from the regression analysis for *Polygonatum pubescens* in order to meet the requirements for a reliable model. Table 4.4 provides information on the allometric equations, and Figure 4.1 to 4.3 illustrate the allometric relationships for each species.

Table 4.4 Allometric relationships between plant size measurements, as predictor variables (x), and total dry biomass, as response variable (Y), for three forest herb species planted in the understory of a mature hybrid poplar plantation

Species	Size variable	Plants harvested (n)	Model	
			$x =$ size measurement (cm)	$Y =$ dry biomass (g)
<i>Asarum canadense</i>	Leaf width (cm)	76	$Y = 0.0236 x^{1.3282}$	0.80
<i>Sanguinaria canadensis</i>	Leaf width (cm)	25	$Y = 0.01819 x^{1.7095}$	0.88
<i>Polygonatum pubescens</i>	Stem length between first and last leaf (cm)	56	$Y = 0.1181 x^{1.1091}$	0.77

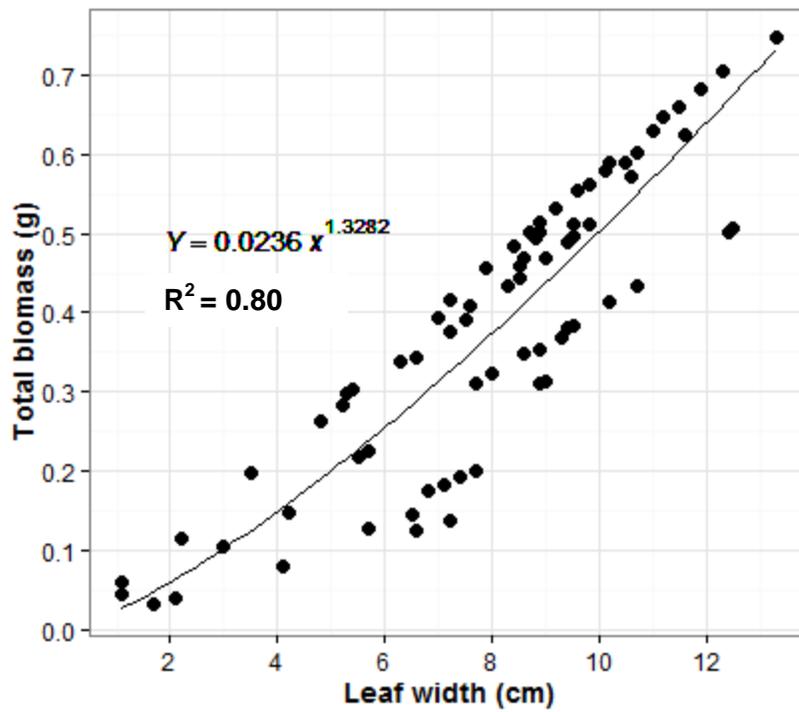


Figure 4.1 Allometric relationship between leaf width (cm) and total dry biomass (g) for *Asarum canadense* planted in the understory of a mature hybrid poplar plantation

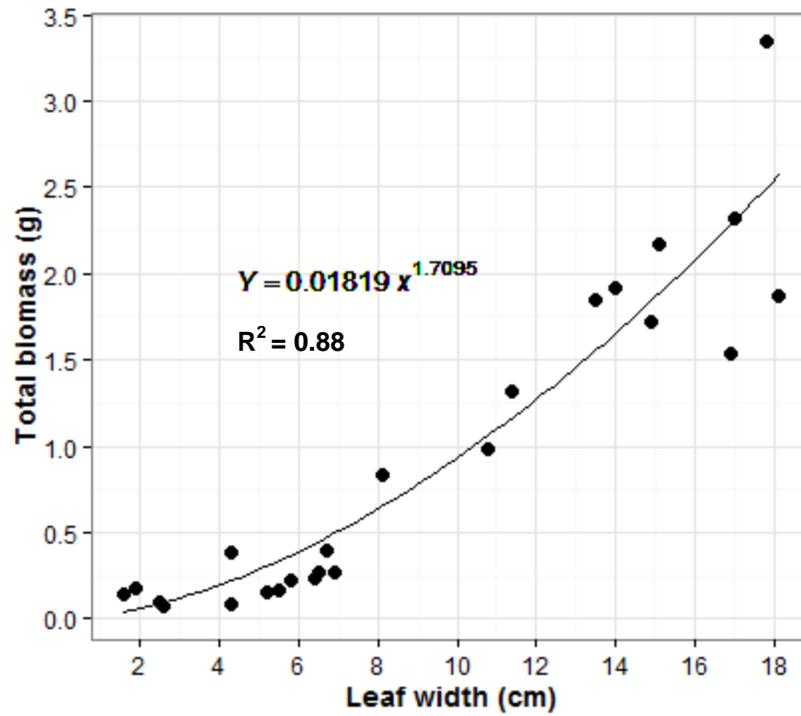


Figure 4.2 Allometric relationship between leaf width (cm) and total dry biomass (g) for *Sanguinaria canadensis* planted in the understory of a mature hybrid poplar plantation

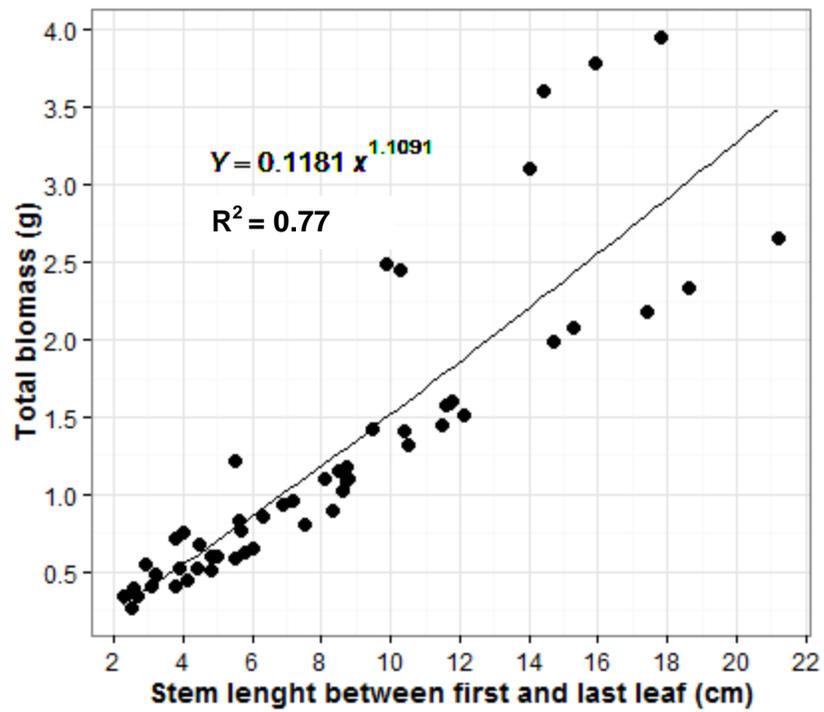


Figure 4.3 Allometric relationship between stem length between first and last leaf (cm) and total dry biomass (g) for *Polygonatum pubescens* planted in the understory of a mature hybrid poplar plantation

### 4.3.3 Results of the forest herb experiment

Although the initial size of the transplants was not uniform within a same species, the initial biomass within each experimental unit (sum of the biomass of all 20 (or remaining) individuals), did not vary significantly between treatments, clone types or blocks. The initial biomass of the transplants was therefore uniform and well-balanced across the experimental design.

Survival was significantly different between species (Table 4.5), and the effect of treatment on survival significantly differed between species (significant interaction Treatment x Species, Table 4.5), supporting our second hypothesis about a different effect of buckthorn depending on the species affected. Survival for the three species was similar under the herbicide treatment (intervals are overlapping), but *Asarum canadense* had a significantly lower survival than the two other species under the control treatment, and in general (when combining the two treatments). Survival rates in control plots were lower on average than in herbicide plots, but this difference was not statistically significant ( $p > 0.05$ , Table 5).

No effects of the block or clone type on plant survival were significant. The effect of buckthorn on plant survival did not differ significantly between clone types (interactions Clone type x Treatment was not significant ( $p > 0.05$ )).

Table 4.5 Mean survival rate per experimental unit of three forest herb species planted in herbicide and control treatments in the understory of a mature hybrid poplar plantation (SAC: *Sanguinaria canadensis*, ASC: *Asarum canadense*, POP: *Polygonatum pubescens*)

	SAC	ASC	POP	Treatment mean	Treatment standard error	Treatment <i>p</i> value
Herbicide	0.88	0.95	0.98	0.94	0.04	0.17
Control	0.95	0.71	0.89	0.85		
Species mean	0.92	0.83	0.94			
Species standard error		0.03				
Species <i>p</i> value		<b>0.05*</b>				

Interaction Treatment x Species significant:  $p = \mathbf{0.0097^{**}}$

\* Significant at  $p < 0.05$

\*\* Significant at  $p < 0.01$

Table 4.6 shows the results of the ANOVA comparing relative growth rates between treatments for each species. After the first growing season in the plantation understory, the relative growth rate of each species was higher in the herbicide plots than in the control plots. The ANOVA showed a weak statistical difference between treatments only at  $p < 0.078$  (Table 4.6). Although not significant at  $p < 0.05$ , these results support our first hypothesis about the overall negative effect of buckthorn on the growth of forest herbs.

Table 4.6 Relative growth rates expressed in terms of total biomass (g/g/year or %) of three forest herb species planted in herbicide and control treatments in the understory of a hybrid poplar plantation (SAC: *Sanguinaria canadensis*, ASC: *Asarum canadense*, POP: *Polygonatum pubescens*)

	SAC	ASC	POP	Treatment mean	Treatment standard error	Treatment <i>p</i> value
Herbicide	48%	26%	129%	<b>68%</b>	0.01	0.078
Control	29%	-20%	90%	<b>33%</b>		
Species mean	<b>39%</b>	<b>3%</b>	<b>109%</b>			
Species standard error		0.08				
Species <i>p</i> value		< 0.001***				

Significant at  $p < 0.001$ \*\*\*

Difference in RGR between species was highly significant (Table 4.6), a result that support our second hypothesis about buckthorn having a different negative effect depending on the species affected. *Asarum canadense* had the lowest mean relative growth rate and was the only species that had a negative mean RGR under the control treatment, where it also had the lowest mean survival rate. *Polygonatum pubescens* had the highest RGR by far, and *Sanguinaria canadensis* had an intermediate RGR to that of the other species.

No effects of the block or clone-type factors were significant. The effect of buckthorn did not differ significantly between species, clone-types or blocks (all interactions, Treatment x Species and Poplar clone-type x Treatment, were not significant ( $p > 0.05$ )).

#### 4.4 Discussion

The environments in the herbicide and control treatments were significantly different in terms of vegetation. Light, soil nutrient and soil humidity conditions were similar between treatments, but vegetation (buckthorn and other understory vegetation) was significantly more abundant in control plots than in herbicide plots. The soil probes were inserted for a month at the beginning of the spring, which is likely to be the moment when the nutrients would have been released and not captured by the removed buckthorns. Moreover, four replicate pairs of soil probes were distributed in each subplot, which is more than the recommended quantity. The absence of a difference in soil nutrient availability between treatments, after the removal in the herbicide plots of 500 g of buckthorn per m<sup>2</sup> on average, suggests that buckthorn does not uptake a significant amount of nutrients. Furthermore, no differences in soil humidity were observed between treatments. These results on soil nutrients and humidity are consistent with the description of glossy buckthorn as a generalist species with low edaphic requirements. Although no differences between treatments were observed in this experimental design for canopy openness, light seems to be the resource that is limited by buckthorn according to the results from a larger experimental design including five clone types from the same plantation (Chapter 3). Because buckthorn is far more abundant than the other understory vegetation in terms of biomass (on average 88% of understory biomass), and because environmental variables are quite constant between treatments, treatment effects on transplanted forest herb growth can plausibly be mainly attributed to buckthorn abundance.

According to one-year growth results, glossy buckthorn appears to have a negative effect on the survival and growth of understory forest herbs. Mean survival and relative growth rates are reduced when buckthorn is present compared to when it is absent. A particularly high mortality that occurred for *Sanguinaria canadensis* in one particular herbicide plot (9 dead individuals on 18 left in 2015) may have prevented the detection of a significant difference in survival between treatments. Half of this problematic plot is located in a shallow depression where water accumulated temporarily in both spring 2014 and spring 2015, as well as after heavy rains during the following summers. In that plot, several *Sanguinaria canadensis* were observed with their stems rotting from the bottom up. This may have counterbalanced the clear trend observed for the two other species, *Asarum canadense* and *Polygonatum pubescens*, of a higher survival rate in the herbicide treatment compared to the control treatment.

The three planted species responded to the new environment (plantation understory) with significantly different survival rates and relative growth rates. *Sanguinaria canadensis* and *Asarum canadense* are listed as vulnerable species in Québec, and they have low population growth rates and high edaphic requirements. Nonetheless, the site corresponds to these two species' common habitat (rich mesic soils under shaded deciduous forest canopies; USDA 2014) and the transplantation area was amended with calcium hydroxide (lime). In addition, the suitability of hybrid poplar plantations for the transplantation of understory herbs, specifically for these two species, has already been confirmed in the experimental hybrid poplar plantation network by a previous study (Boothroyd-Roberts et al. 2013a). Therefore, instead of being related to the site conditions, differences in RGR may rather reflect specific growth patterns. *Sanguinaria*

*canadensis* and *Asarum canadense* share a similar plant form, which differs from the plant form of *Polygonatum pubescens*. In terms of survival, the effect of buckthorn significantly differed between species (significant Treatment x Species interaction). This indicates that the differences in survival between species significantly relate to the specific susceptibility to a negative buckthorn effect by each of the three forest herb species. It is normal to observe mortality in the first few years following transplantation (Mottl et al. 2006), but the significance of the interaction in the analysis shows that buckthorn increases mortality rates for some species. It is however surprising to observe that *Sanguinaria canadensis* and *Asarum canadense*, which have a similar growth form and edaphic requirements, responded to the buckthorn effect with different survival rates. A possible explanation may be that *Sanguinaria canadensis* tolerates humid soils better than *Asarum canadense*. Although *Sanguinaria canadensis* is known to grow on well-drained soils, it is also found in flood plains, on shores or near streams (FNA 2014). Because the plantation used in the current study has a locally imperfect soil drainage, it is possible that the effect of buckthorn on *Asarum canadense* was stronger because it represents an additional stress when coupled with high soil moisture.

Blocks and clone-type canopies did not have very different environments and their effects on forest herb survival and growth were not detected by the analyses. First, forest herb mortality and growth did not significantly differ between blocks, although there were some significant differences in the canopy openness and buckthorn abundance between blocks. This is maybe due to the blurred gradient in buckthorn abundance. Although buckthorn follows a significant increasing gradient in density from block 1 to 3, total buckthorn biomass does not seem to follow any trend. In fact, buckthorn biomass is

at its lowest in block 2, where canopy openness at 1 m above ground level is the highest. Canopy openness also does not follow any gradient between blocks, but was significantly different between blocks. It is possible that the effect of buckthorn on forest herbs does not vary within the range of the tested buckthorn densities (1 to 3 stems/m<sup>2</sup>).

The two hybrid poplar clone types tested did not result in significantly different understory environments, and did not result in significant differences in forest herb RGR and survival. The two hybrid poplar clone types did not produce a significantly different wood volume or biomass, the environmental conditions in their understory were not significantly different (soil nutrient availability, soil humidity, canopy openness at 3 m), and the understory vegetation biomass (buckthorn and other species) did not differ significantly between them. Clone-type canopy only had a significant effect ( $p < 0.05$ ) on canopy openness at 1 m above ground level, under most of the buckthorn cover. This appears to be a spurious effect, because clone type canopy did not have an effect on canopy openness at 3 m above ground level, above most of the buckthorn cover. Moreover, no other related variables, such as buckthorn density or biomass, followed a similar trend. Our third hypothesis, about the potential of hybrid poplar clone canopy influencing buckthorn or its effect on understory forest herbs, is therefore rejected. Boothroyd-Roberts et al. (2013) also did not observe any significant difference in environmental variables between hybrid poplar clone type canopies ten years after their plantation.

#### 4.5 Conclusion

Only a few studies on buckthorn have included forest herbs. However, in these studies, the response to buckthorn was measured only on overall herb cover and on species richness. This experiment is to our knowledge the first one to use transplants, therefore giving valuable information on restoration and cultivation issues with buckthorn, in addition to measuring the effect of buckthorn directly on individual plants. A reduction in growth was observed under buckthorn cover and the effect of buckthorn appears to be stronger on some species than on others. Finally, this study is the first one to study the effect of buckthorn on forest herbs in Canada, and in a plantation that is very similar to early successional, partially open forests, which are common throughout the Northern Hardwoods forest region.

Glossy buckthorn clearly has a negative effect on understory forest herbs by reducing their survival and growth, after one year of growth in the experimental design. This effect on survival varies from species to species. When forest herbs are transplanted for cultivation or restoration purposes, special attention should be given to the selection of the species used. The effect of buckthorn may be increased on transplants that are already stressed by environmental conditions. Therefore, transplants that are larger in size and species that are well adapted to the transplantation site should be selected in priority for such projects. In a similar manner, we expect that glossy buckthorn will stress fragile herb populations in natural habitats, and negatively affect their growth and survival.

Observations from an additional growing season in June 2016 will allow us to determine how this negative effect of buckthorn evolves with time. We expect this effect to become stronger and significant for both growth and survival. Our results relative to environmental factors do not allow us to determine if glossy buckthorn is a driver of

change in the environment tested. A longer observation period and/or a larger experimental design may be necessary to assess such changes. A larger experimental design used for a similar experiment on tree seedlings (Chapter 3) allowed us to observe a significant reduction in canopy openness (a proxy for light availability) when buckthorn is present compared to when it is absent. This offers an explanation for the reduced growth and survival rates observed for forest herbs in this experiment. The effect observed on forest herbs also suggests that, over the long term, significant changes in composition in the understory flora would occur.

Based on the results from this study, and on those of a negative effect on tree seedlings obtained in a similar experiment on tree seedlings (Chapter 3), we can conclude that buckthorn has a negative impact on native species in plantation of natural forest understories. Therefore, the monitoring and control of this invasive species should be a priority for forest managers. Results from this study support the description of glossy buckthorn as a species with low edaphic requirements, which justifies the concern that this species could invade a very wide range of ecosystems, including those where rare, threatened or endangered plant species occur.

## CHAPTER FIVE: General conclusion

This study has increased our understanding of the ecology of glossy buckthorn, it provides experimental evidence of a negative effect of buckthorn on native tree seedlings and forest herbs, it provides evidence on which factors cause this negative effect, and it shows that the effect of buckthorn differs from species to species. The research presented here is also unique because of its use of transplants, of both tree seedlings and forest herbs, and because of its sound experimental design, measuring several factors, established in an experimental plantation naturally invaded by glossy buckthorn. This research project took place in southern Québec, in a mature hybrid poplar plantation that is comparable to early successional, partially open hardwood forests that are common throughout southeastern Canada.

The results of this thesis confirm the invasive potential of glossy buckthorn in both open and forested habitats, due to its use of different architectural strategies that are adapted to the amount of light available. We also observed densities of first-year buckthorn seedlings which are much higher than the highest count reported in the literature, which is up to 700 seedlings/m<sup>2</sup> compared to the 100 seedlings/m<sup>2</sup> previously observed by Godwin (1943). Moreover, our results confirm the low edaphic requirements of buckthorn, which support the concern that it can invade a very wide range of ecosystems, including those where rare, threatened or endangered plant species occur. Additionally, we observed a rapid growth rate for the first-year buckthorn seedlings germinating after the herbicide treatment was applied in the treatment plots. This lends support to the concern that buckthorn could easily re-invade and perhaps outgrow native plants after a herbicide is used as a treatment to remove buckthorn.

Our short-term results on buckthorn seedling density and growth rate, and on the negative effect of buckthorn on native tree seedling and forest herb growth provide support for the rapid reforestation of sites that have been recently cleared and treated with herbicide, and more generally of sites that have a partially open canopy and moderately well to imperfectly drained soils. Relying on natural regeneration in these situations may be ill advised, especially in the highly fragmented landscapes typical of southeastern Canada, where remaining surrounding forested areas are often distant. Colonization success by native species depends on these remaining forest fragments for seed sources. Reforesting (after agricultural abandonment or clear cutting) or under-planting (in appropriate early successional stands or mature poplar plantations) appears to be necessary in order to outpace buckthorn colonization.

Restoration of valuable hardwood species, by under-planting in young low-density early successional forests or by planting on abandoned farmland, is currently promoted by forest managers in southern Québec, where over 200,000 hectares hold a potential for either under-planting or plantation of valuable hardwood species. However, our results suggest that the presence of glossy buckthorn has a negative effect on their success. We observed a negative effect of buckthorn on planted tree seedling and forest herb growth, and we conclude that shading by buckthorn produces this effect. A decrease in light availability in the understory, caused by buckthorn, could lead to an altered canopy tree composition and to modifications in species distribution in the future. Although shade-tolerant tree species, such as sugar maple, may be able to grow in the presence of buckthorn, albeit poorly, other species with higher light requirements, such as red oak or white ash, may have large growth reductions and have great difficulty surviving the

buckthorn filter. Sugar maple is very rarely planted because it is abundant in naturally regenerated forests. Red oak, however, is a species of choice for under-planting and for establishing plantations. Therefore, our results have important implications for the restoration of red oak under partial tree cover if buckthorn has invaded the understory. Efforts need to be directed towards devising effective control methods for buckthorn, and developing special management practices for restoration (under-planting) and reforestation projects that take the presence of buckthorn into consideration.

The negative effects observed on forest herb survival and growth, which vary among species, suggest that over the long term important changes in the composition of the herbaceous understory flora could also occur. In addition, the effect of buckthorn may be increased on herbaceous plants that are already stressed by changing environmental conditions. Glossy buckthorn may be especially detrimental to some fragile herbaceous plant populations in natural habitats, and negatively affect their growth and survival. Using larger plants for transplanting, and species with ecological requirements that closely match those of the transplantation sites, would increase the success of future forest herb restoration or cultivation projects (non-timber forest products).

Although it took quite some time before glossy buckthorn abundance was considered a serious issue in North America (Catling and Mitrow 2012), our results contribute additional scientific evidence supporting the hypothesis of a negative effect of buckthorn on Eastern North American forest understories, and emphasize the urgency of classifying glossy buckthorn as a priority invasive species for control. Moreover, we should be conscious that we may not yet have a complete idea of buckthorn's potential range of invasion, because the species is still spreading. It is impossible to currently assess if its

present range is limited by northern climatic conditions or by a lack of propagules (Reich et al. 2015). In addition, a study on the predicted changes in the distribution ranges of tree species in response to climate change concluded that boreal tree species, dominant in their current colder range (due to a trade-off between tolerance to cold and growth capacity), would probably respond not as well to warmer conditions, and would probably be more sensitive to droughts and less competitive than temperate tree species with more southern distribution ranges (Reich et al. 2015). This study also concluded that temperate species, including common buckthorn (an introduced invasive species which shares many traits with glossy buckthorn), oaks and maples, had increased photosynthesis and growth rates in response to an experimental simulation of climate change (e.g. warming). It can therefore be suggested that both introduced buckthorn species, oaks and maples will be expanding their range further north with climate change (Reich et al. 2015). If no special management practices or control methods are developed, our results provide an indication of which of these species' seedlings will likely do best in taking advantage of these predicted future modifications in species ranges.

It is likely that dense populations of buckthorn will hinder most native hardwood tree seedlings in their growth and survival, to levels that differ among species. Higher light demanding seedlings, such as those of red oak, will be the most severely affected.

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