Forests **2015**, *6*, 1083-1093; doi:10.3390/f6041083

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Communication

Aboveground Biomass of Glossy Buckthorn is Similar in Open and Understory Environments but Architectural Strategy Differs

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Academic Editors: Shibu Jose and Eric J. Jokela

Received: 12 February 2015 / Accepted: 2 April 2015 / Published: 8 April 2015

Abstract: The exotic shrub glossy buckthorn (*Frangula alnus*) is a great concern among forest managers because it invades both open and shaded environments. To evaluate if buckthorn grows similarly across light environments, and if adopting different shapes contributes to an efficient use of light, we compared buckthorns growing in an open field and in the understory of a mature hybrid poplar plantation. For a given age, the relationships describing aboveground biomass of buckthorns in the open field and in the plantation were not significantly different. However, we observed a significant difference between the diameter-height relationships in the two environments. These results suggest a change in buckthorn's architecture, depending on the light environment in which it grows. Buckthorn adopts either an arborescent shape under a tree canopy, or a shrubby shape in an open field, to optimally capture the light available. This architectural plasticity helps explain a similar invasion success for glossy buckthorn growing in both open and shaded environments, at least up to the canopy closure level of the plantation used for this study.

Keywords: *Frangula alnus*; plasticity; invasive species; southern Québec (Canada); biomass equation; light availability

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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 [1]. 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 [2,3]. Buckthorn is generally not considered particularly shade tolerant. However, it is observed to invade both open and understory environments [4–6]. The question is how this occurs. In forest understories, buckthorn may out-compete native species, especially in the colonization of canopy gaps.

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.* [7] 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. A first 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 [2,8–10]. Indeed, Mills *et al.* [10] 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 [7]. Moreover, the seeds of glossy buckthorn have a high germination rate, and buckthorn has low ecological requirements [10] and a rapid growth rate [7,9,11]. 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 [10].

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 the use of 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 age. 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 biomass production potential. We also tested if the diameter-height relationships for buckthorns from both environments were significantly different. If the relationships are different, it shows that glossy buckthorn is capable of a certain plasticity in its architecture, as also seen in other species [12]. 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. Methods

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 (Latitude 45.265153° N; Longitude 72.045232° W), 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*) [13]. 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 [14]. 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 [14]. 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 × 40 m). Hybrid poplars were spaced 3 m × 4 m apart, for an initial density of 833 stems/hectare [14]. The average diameter at breast height of the hybrid poplars was 23.5 ± 5.6 cm (mean ± standard deviation) in 2014, and the basal area of the plantation was 22 m^2/ha. Hybrid poplar biomass measurements required the harvesting of 30 trees (15 in 2007, and 15 in 2012) [14,15]. 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 Version 2.0 (Burnaby, Canada, Millbrook, USA) [16]). A natural gradient in glossy buckthorn density, measured in 2014, from block 3 (7 stems/m^2; buckthorn most likely first invaded plantation through this block) to block 1 (2 stems/m^2) 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. 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, see Figure 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 (see Figure 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.

Figure 1. Hybrid poplar plantation understory with abundant glossy buckthorns.

Figure 2. Harvested buckthorn stem cross section showing growth rings.

An aboveground predictive equation of biomass (woody parts plus leaves) (Y) was developed for each environment (open field and plantation), using basal diameter as predictor variable (x). 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 analyses of covariance (ANCOVA) 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, height or basal diameter. 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 (31 October 2014), Vienna, Austria).

3. Results and Discussion

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 1, Figure 3).

Table 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

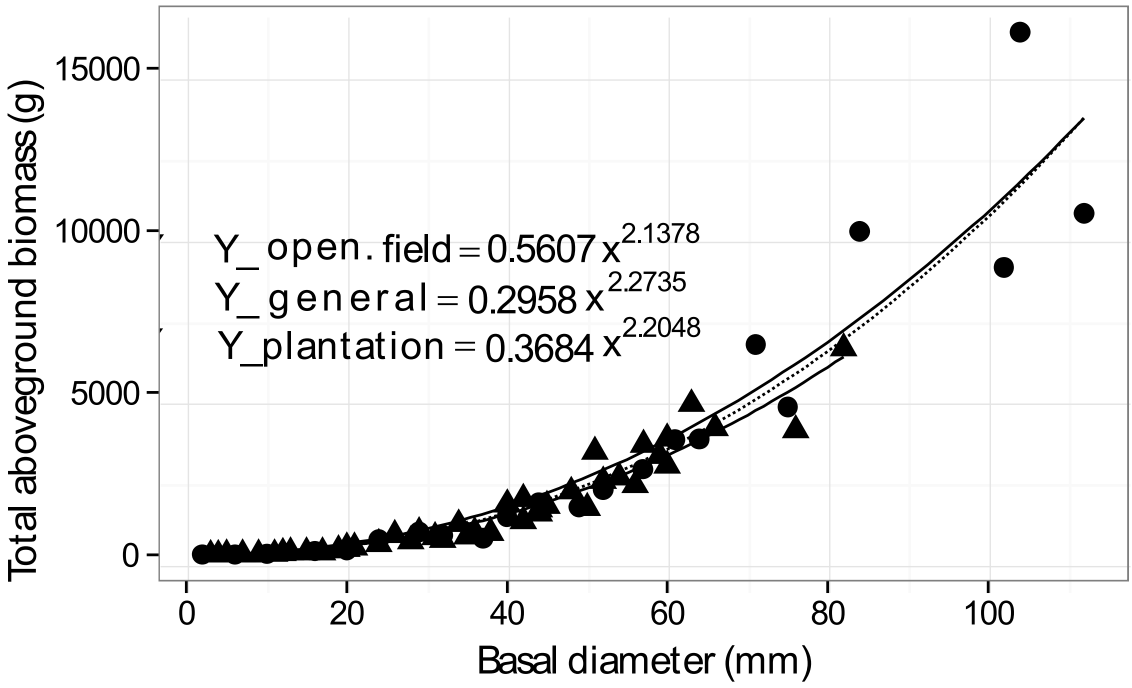

Figure 3. Environment-specific relationships and general allometric relationship for glossy buckthorn between basal diameter (mm) and total aboveground biomass (g). Triangle symbols = Plantation data points; Circle symbols = Open field; Dotted line = general model (plantation + open field).

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 1). These equations will be the most useful for forest managers because their use allows biomass calculations to be made without destructive sampling. The general equation is appropriate to use in both open and shaded environments, because we did not find a significant difference between the relationships for the two environments ($p = 0.1244$).

We first tested the relationships describing age *vs.* total aboveground biomass of buckthorns in the open field and in the plantation, and they were not significantly different (Table 2, see Figure 4 for age and total aboveground biomass relationships).

We then tested for a difference in the diameter-height relationships for buckthorns in the two environments and observed that they were significantly different (Table 2, see Figure 5 for diameter-height relationships).

Table 2. Significance levels (*p*-values) for the non-parametric analyses of covariance (ANCOVA) testing for a difference in the relationships for the two environments between age, basal diameter or height, as predictor variables and aboveground biomass, height or basal diameter as response variables.

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 $p < 0.05$.

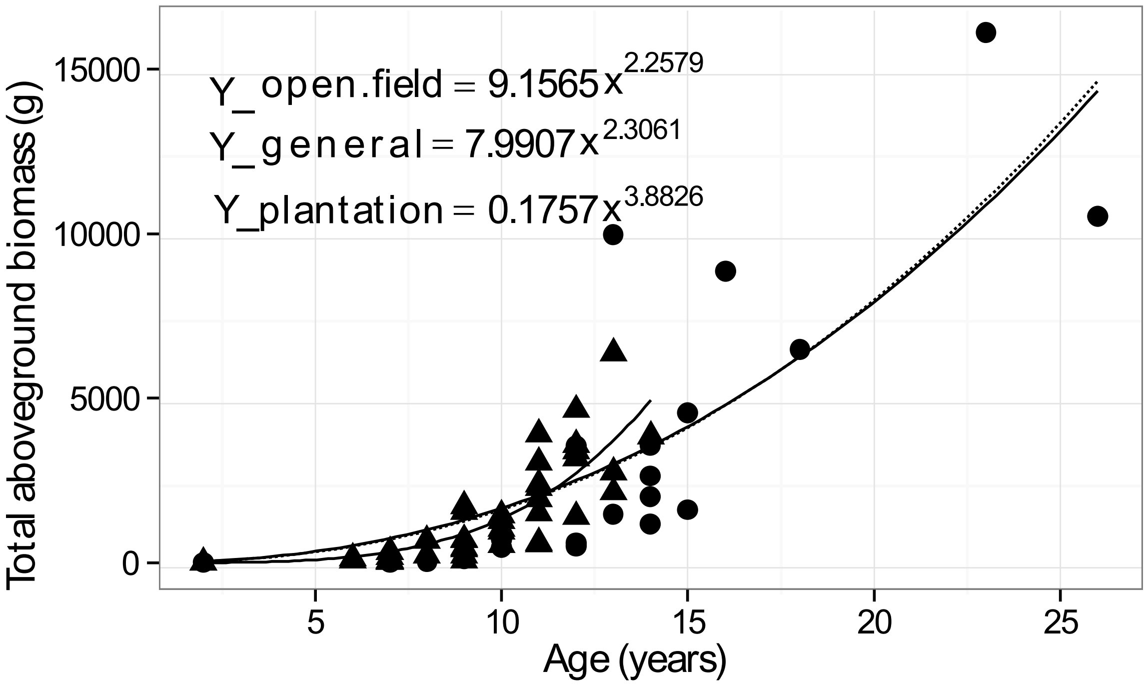

Figure 4. Environment-specific relationships and general allometric relationship for glossy buckthorn between age (years) and total aboveground biomass (g). Triangle symbols = Plantation data points; Circle symbols = Open field; Dotted line = general model (plantation + open field).

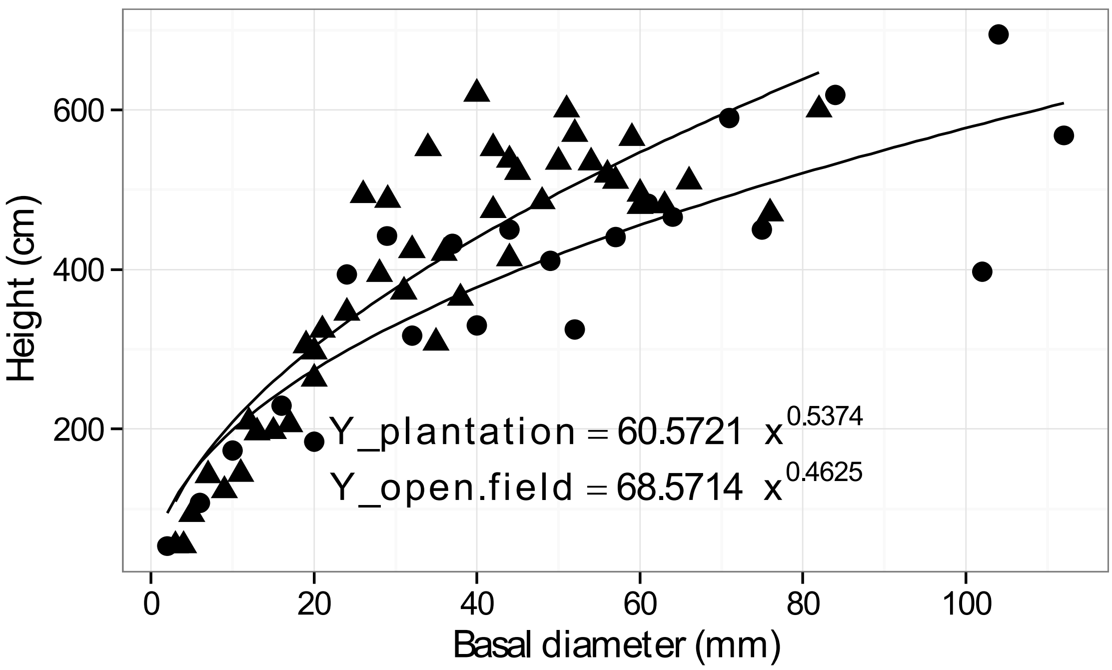

Figure 5. Environment-specific allometric relationships for glossy buckthorn between basal diameter (mm) and height (cm). Triangle symbols = Plantation data points; Circle symbols = Open field.

Therefore, at a given age, buckthorns in the plantation and in the open field will have reached a similar total aboveground biomass (Figure 4, Table 2: $p = 0.5025$), but significantly different heights (Table 2: $p = 0.01$) and diameters (Table 2: $p = 0.0199$).

The significant difference observed between diameter-height relationships in the two environments (Figure 5, Table 2, $p = 0.0149$) suggests a change in buckthorn architecture. From Figure 5, we can see that for the same basal diameter of 60 mm, plantation understory buckthorns will be 100 cm taller than open field buckthorns. We observed that glossy buckthorn follows two different architectural patterns that are consistent with the ones described by Charles-Dominique *et al.* [17] for common buckthorn (*Rhamnus cathartica* L.), a species similar to glossy buckthorn in many respects.

Charles-Dominique *et al.* [17] 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 6). 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" [18]. This state would be reversible if conditions change. In contrast, in an open area, buckthorn adopts a shrubby shape, using short modules and abundant branching to take space in the shrub stratum [17] (see Figure 7).

Figure 6. Arborescent architecture of glossy buckthorn in plantation understory.

Figure 7. Shrubby architecture of glossy buckthorns in open field.

The similar amount of biomass produced for a same age 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 terms of biomass production 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 that of naturally regenerated woodlots (second-growth forests) dominated by hardwood species (approximately 12% openness) [19]. Considering that several authors observed that light is a limiting factor in the spread of glossy buckthorn [1,4,9], our study plantation may not have yet reached the threshold of canopy closure over which the photosynthetic performance of buckthorn is altered. It was observed by Luken and Goessling [20] for *Lonicera maackii*, another invasive shrub, that there was a decreasing invasion success from forest edges (which could have light conditions comparable to that of our study plantation) to forest interiors.

Furthermore, Sanford *et al.* [7] 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.* [7] 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 [4,21]. 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 [22].

4. Conclusions

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

Acknowledgments

Research funding to the Eastern Townships Forest Research Trust by the Ministère des Forêts, de la Faune et des Parcs du Québec ("Chantier sur la forêt feuillue" Program) is gratefully acknowledged. We thank Amélie Lacroix-Dehours and Daniel Hamelin for their assistance in the field. We also thank owners Caroline Iannuzzi and Frédéric Nadeau for allowing this research project to occur on their property. We also wish to thank Harry Isbrucker for providing us with ample space for sample preparation and drying. We are grateful to Dr. Julien Fortier for his review of the statistical analyses and for his advice. Caroline Hamelin gratefully acknowledges graduate scholarships received from the Fonds de recherche du Québec—Nature et technologies, from the Eastern Townships Forest Research Trust, and from the Faculty of Graduate Studies and Research of the University of Regina. Finally, we wish to thank two anonymous reviewers whose positive and constructive comments have helped to improve this paper.

Author Contributions

Caroline Hamelin collected and analyzed the data, and drafted the manuscript. Daniel Gagnon and Benoit Truax contributed in designing the experiment, helped coordinate the data collection and assisted with data analyses and the review of the manuscript. Benoit Truax selected the study site, designed and established the experimental hybrid poplar plantation. All three authors participated in the conception and design of the study and read and approved the final manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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