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Abstract

Many ecosystems are now dominated by introduced species, and because dominant species drive ecosystem properties, these changes lead to increased uncertainty in estimates of carbon storage and cycling. We examined aboveground biomass in forests dominated by the introduced tree *Rhamnus cathartica* (common

buckthorn) relative to forests dominated by native species, and measured aboveground biomass increment over a three-year period (2005–2008). Three of the four lowest biomass levels occurred in *R. cathartica*-dominated forests, and biomass in these forest types was stored primarily in trees 10–20 cm DBH. By contrast, forests dominated by native trees (including those with *R. cathartica* understories) had the six highest biomass levels, and biomass was stored primarily in trees >50 cm DBH. On average, forests dominated by *R. cathartica* stored half as much aboveground biomass (14.6 ± 3.3 kg/m^2) as forests dominated by native tree species (28.9 ± 8.3 kg/m^2). *R. cathartica*-dominated forests also had half the aboveground biomass increment of native-dominated forests (0.28 vs. 0.60 kg/m^2/year). Although known anecdotally as a fast-growing species, *R. cathartica* growth rates declined with increasing size. Between 2005 and 2008, *R. cathartica* individuals <10 cm DBH grew faster than native species; however, *R. cathartica* individuals >10 cm DBH grew consistently slower than native species. Overall, our findings indicate that intrinsic size limitations on *R. cathartica* will lead to lower biomass stocks in forests where it acts as a canopy dominant relative to forests dominated by native tree species.

Research highlights

→ Forests dominated by *Rhamnus cathartica* stored half the biomass of those dominated by native trees. → Growth of *R. cathartica* declined relative to native trees with increasing size. → Allometric models provided for biomass, height, leaf biomass, and fruit biomass of *R. cathartica*.

1. Introduction

A key driver of changing species composition is the global proliferation of introduced species. In fact, a large group of ecosystems are now dominated by introduced species ([Lugo, 2004](#), [Hobbs et al., 2006](#), [Mascaro et al., 2008](#)). Because dominant species drive ecosystem properties ([Ellison et al., 2005](#)), widespread changes in dominance lead to great uncertainty in estimates of carbon storage and cycling. There is evidence that productivity and aboveground biomass increase following invasion, but the effects often depend on species-specific characteristics (reviewed by [Ehrenfeld (2003)](#)). For instance, the large introduced tree *Falcataria moluccana* (albizia) dramatically alters forest structure in Hawai'i, sometimes increasing canopy height and biomass by a factor of five ([Hughes and Denslow, 2005](#)). In a similar forest, however, exotic grasses and small trees replace large native trees and dramatically reduce biomass ([Hughes et al., 1991](#), [Litton et al., 2006](#), [Asner et al., 2008](#)). In each case, the relative change in dominant plant form and size has a large impact on biomass storage. Thus, quantifying changes to carbon dynamics that are caused by introduced species will depend in part on an understanding of the allometries of the introduced species relative to those they are replacing.

Rhamnus cathartica (common buckthorn) is a widespread introduced tree in various habitats in the Upper Midwest and Northeastern US as well as Central and Eastern Canada and is listed as a prohibited or restricted weed in several US states ([Knight et al., 2007](#), [USDA, 2010](#)); it can act as a canopy dominant in Southern Wisconsin, forming monotypic stands and exceeding the level of relative dominance reached by most other woody invaders of eastern temperate forests ([Mascaro and Schnitzer, 2007](#)). Because *R. cathartica* is widespread and capable of dominating forest ecosystems, its influence on aboveground carbon storage (i.e., approximately 48% of dry biomass) relative to forests dominated by native trees is of considerable importance. Here, we contrast how aboveground biomass is stored structurally over a range of tree diameter classes in ecosystems lacking *R. cathartica*, those with *R. cathartica* understories, and those dominated in the canopy by *R. cathartica*. We also examined biomass dynamics by contrasting aboveground biomass increment at the stand level, and compared *R. cathartica* growth to that of native species over a three-year period.

To facilitate our investigation of aboveground biomass patterns in forests with *R. cathartica*, we developed allometric models for predicting height, aboveground biomass, and leaf and fruit biomass based on stem diameter. A previous study developed allometry for shrub-form *R. cathartica* individuals ≤3.2 cm in basal

diameter ([Harrington et al., 1989b](#)). In our study area, however, *R. cathartica* exhibits a tree habit, and commonly reaches 25 cm in diameter.

2. Methods

2.1. Study area and sampling methods

The study area was 16 wet to mesic forest sites in Southern and Southeastern Wisconsin (a map of the sites, and additional site information can be found in [Mascaro and Schnitzer, 2007](#)). Eight of the sites are dominated by native hardwood trees in the canopy (e.g., *Acer rubrum*, *Fraxinus americana*, *Populus deltoides*), and in the understory (e.g., *Prunus virginiana*, *Ostrya virginiana*). Four sites have a native-dominated canopy with abundant *R. cathartica* in the understory, while four sites were dominated by *R. cathartica* in the canopy and understory (i.e., 50–100% of basal area). Aerial photography revealed that two of the four *R. cathartica*-dominated sites had been in closed canopy forest since at least 1963 while the other two had open canopies in 1975 ([Mascaro and Schnitzer, 2007](#)). Native-dominated forests (including those with *R. cathartica* understories) were somewhat older on average, with three of 12 having open canopies in 1975 and the remainder closed since 1963. In July–September 2005, we established four 6 m-radius circular plots at each site (stratified among sites, random within sites), with 18 m between adjacent plots (0.045 ha total area). At one site, where *R. cathartica* was particularly abundant, vegetation was sampled in only two plots (0.022 ha total area); the number of stems sampled at this site exceeded that at any other. Within each plot, we measured and identified all trees ≥1 cm DBH, and mapped and marked each genet with a uniquely numbered aluminum tag. Ramets (clonal stems attached to genets below 1.3 in height) were measured for biomass but were not tagged. Three years later, in August 2008, we recensused 15 of the 16 sites. One of the native sites was inaccessible due to heavy flooding and data from this site are included in standing biomass estimates but not the increment or growth analyses.

2.2. Biomass estimation and growth calculation

We destructively harvested 15 individuals ranging from 1 to 25 cm DBH and spread across 5 sites where *R. cathartica* was common in the understory or canopy. We separated each individual into four tissue categories: leaves, stems <1 cm, stems ≥1 cm, and fruit. Each pool was weighed and subsamples were collected and dried to constant mass at 60 °C in a forced air oven to correct for moisture content. We combined the four tissue categories to determine aboveground biomass. The resulting equation (see Section [2.3](#)) was used to estimate the standing aboveground biomass of all *R. cathartica* individuals. For several other species (41% of non-*R. cathartica* basal area), we used species-specific allometric regression equations compiled by [Jenkins et al. (2001)](#). For species with no available equations (59% of non-*R. cathartica* basal area), we followed the method of [Jenkins et al. (2001)](#) and substituted equations of species with similar wood density. Lianas constituted <1% of basal area and thus were not included in biomass estimates. We calculated standing biomass of live stems (i.e., both genets and ramets), and summed the total biomass for each site.

We examined biomass estimates from the 2005 data among three site types based on the level of *R. cathartica* dominance: (1) native-dominated sites with native understories, (2) sites with native canopies but *R. cathartica* understories, and (3) sites where *R. cathartica* dominated the canopy and understory. To examine variation in forest structure, we further divided biomass stocks by 10-cm DBH size classes. Based on the structural similarity between the native sites and those with *R. cathartica* understories (see Section [3](#)), we tested whether *R. cathartica* dominance significantly affected aboveground biomass and its increment (biomass accumulation in all surviving stems over the three-year census interval; follows method 1, [Clark et al., 2001](#)) by comparing native-dominated sites (groups 1 and 2) to sites dominated in the canopy by *R. cathartica* (group 3).

We considered the possible influence of tree growth rates on biomass dynamics over time by calculating the absolute growth of all individuals over the three-year period by subtracting stem diameter in 2005 from stem diameter in 2008 for the largest stem of each genet. We compared *R. cathartica* growth to the growth of all other species combined, regardless of site type.

2.3. Statistical analyses

We used linear regression to correlate stem diameter of harvested *R. cathartica* individuals to height, whole-plant aboveground biomass, leaf biomass, and fruit biomass (SigmaPlot, 2006). For each equation, we used a linear function of the form:

$$(1) \quad \ln(y) = \ln(a) + b\ln(x)$$

where *y* is the dependent variable (e.g., height or biomass), *x* is the independent variable (e.g., diameter), and *a* and *b* are regression coefficients. Each equation was then back-transformed to a power function of the form:

$$(2) \quad Y = ax^b \times \text{CF}$$

where CF is a correction factor computed as:

$$(3) \quad \text{CF} = e^{(\text{MSE}/2)}$$

and MSE is the mean squared error of the regression. The CF accounts for the back transformation of the regression error (Baskerville, 1972, Chave et al., 2005).

Site-level aboveground biomass was not normally distributed (Shapiro–Wilk *W* test, *P* = 0.0358) and thus we compared aboveground biomass and its increment (for consistency) among sites using non-parametric statistics (R Core Development Team, 2009). After an initial analysis (see Section 3) revealed structural similarity among sites dominated by native canopy trees (including those with *R. cathartica* understories), we compared aboveground biomass and its increment between sites dominated in the canopy by native trees (*n* = 12 for biomass, 11 for increment) and those dominated in the canopy by *R. cathartica* (*n* = 4) using a Mann–Whitney *U* test.

3. Results

R. cathartica stem diameter was a good predictor of height, leaf biomass, fruit biomass, and total aboveground biomass (Table 1 and Fig. 1). The relationship between diameter at breast height and aboveground biomass was particularly strong (r^2 = 0.9975). Stem diameter at the ground (a measurement used commonly for shrub allometry; e.g., Litton and Kauffman, 2008) was also a strong predictor of aboveground biomass (r^2 = 0.9937). Compared to allometric models for other species groups (sensu Jenkins et al., 2001) found in this study, *R. cathartica* fell in the middle of the range, but had a shallower slope than most (Table 2). Ten of 11 equations underpredicted the aboveground biomass of *R. cathartica* at 5 cm DBH, while 9 of 11 equations overpredicted its biomass at 25 cm DBH (near its maximum size).

Table 1. Allometric equation coefficients for *Rhamnus cathartica* L. (common buckthorn) based on diameter, height, and the oven-dry weights of various plant parts of 15 harvested individuals from 5 sites in Southern Wisconsin.

Equation	x	y	a	b	r^2	N	Range	CF	MSE
1	DBH (cm)	Ht (m)	2.9740	0.4503	0.92	15	1.2–24.7	1.0105	0.0209
2	DBH (cm)	AGB (kg)	0.1692	2.2904	0.99	15	1.2–24.7	1.0074	0.0148
3	DBH (cm)	Leaf biomass (kg)	0.0287	1.6046	0.94	15	1.2–24.7	1.0937	0.1792
4	DBH (cm)	Fruit biomass (g)	1.1190	2.1790	0.98	5	1.4–18.2	1.0890	0.1705
5	Ground diameter (cm)	AGB (kg)	0.0638	2.4408	0.99	15	1.9–30.2	1.0190	0.0377

Notes: All equations were developed using ln-transformed data and simple linear regression, after which equation coefficients were back-transformed to a power function of the form $y = ax^b \times CF$, where x is the independent variable, y is the dependent variable, a and b are equation coefficients, and CF is a correction factor accounting for the back transformation of the regression error ([Baskerville, 1972](#)). MSE is the mean squared error of each linear model, r^2 is the coefficient of determination, AGB is aboveground biomass (kg), and DBH is the diameter at 1.3 m from the ground (cm). The *P*-value of Eq. (4) was 0.0015; all others were <0.0001. Only the 5 fruiting individuals were used to generate Eq. (4), and this equation should be used only for fruiting trees.
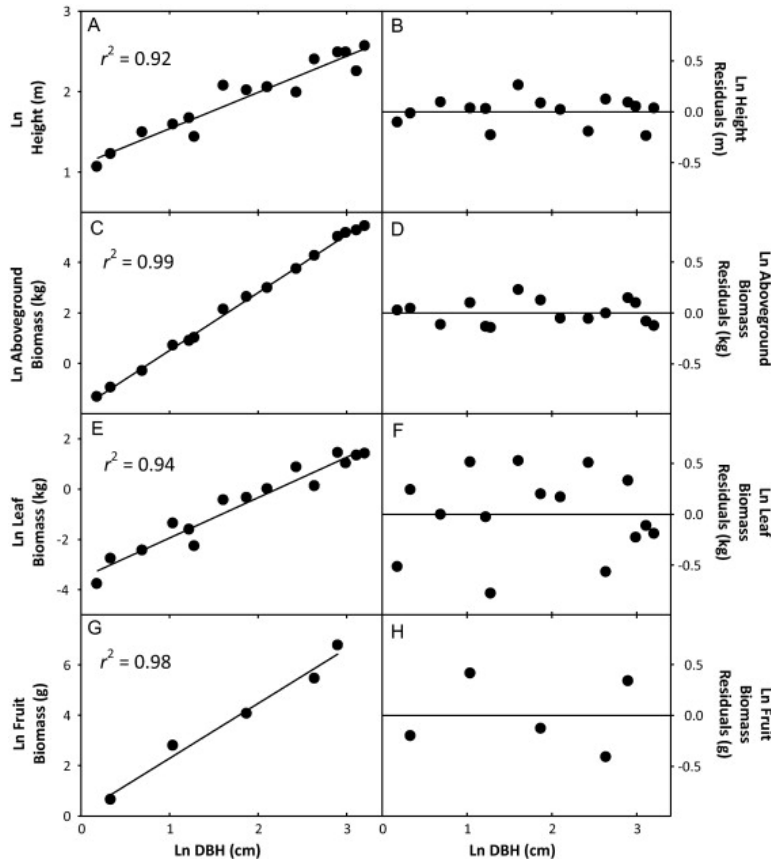

Fig. 1. Allometric relationships and residuals between (a and b) diameter and height, (c and d) diameter and aboveground biomass, (e and f) diameter and leaf biomass, and (g and h) diameter and fruit biomass for *Rhamnus cathartica* (common buckthorn). See [Table 1](#) for equation coefficients.

Table 2. Percent difference in predicted aboveground biomass (kg) between several species groups (sensu Jenkins et al., 2001) and a model presented for R. cathartica (Table 1 and Fig. 1). Following the Jenkins et al. (2001)classification, most North American shrubs and small trees are grouped with Acer rubrum, Prunus serotina, and Quercus alba.

Species group	Diameter (cm)				

	5.0	10.0	15.0	20.0	25.0
Acer rubrum	−14.5	−9.0	−5.6	−3.1	−1.2
Acer saccharum	−12.6	34.1	44.1	45.0	43.2
Carya spp.	−23.9	−4.3	9.4	20.3	29.5
Fagus grandifolia	3.7	34.5	40.7	40.2	37.8
Fraxinus americana	−0.5	22.7	25.1	23.1	20.1
Liriodendron tulipifera	−42.2	−32.5	−26.0	−21.1	−17.0
Populous spp.	−37.6	−22.2	−11.5	−3.1	4.1
Prunus serotina	−10.8	−2.1	3.4	7.5	10.8
Quercus alba	−46.5	−28.8	−15.9	−5.4	3.7
Quercus coccinea	−7.5	2.5	8.9	13.7	17.5
Quercus rubra	−31.8	−11.9	2.4	13.9	23.6
Mean	−21.0	−0.8	8.1	13.4	17.3

A visual analysis of forest structure revealed that *R. cathartica*-dominated sites lacked large trees (>50 cm DBH) entirely ([Fig. 2](#)). Aboveground biomass was significantly higher in forests dominated by native canopy trees (including those with *R. cathartica* understories) than those dominated in the canopy by *R. cathartica* (Mann–Whitney U test, $P = 0.0418$). At the four sites where relative *R. cathartica* basal area ranged from 50 to 100%, two had the lowest standing biomass stocks (each 10 kg/m^2), and a third site ranked fourth from the bottom (14 kg/m^2). The *R. cathartica*-dominated site with the highest aboveground biomass fell on the low end of overall range (24 kg/m^2; range 10–63 kg/m^2). On average, forests dominated by *R. cathartica* stored half as much aboveground biomass (14.6 ± 3.3 kg/m^2) as forests dominated by native tree species (28.9 ± 8.3 kg/m^2).
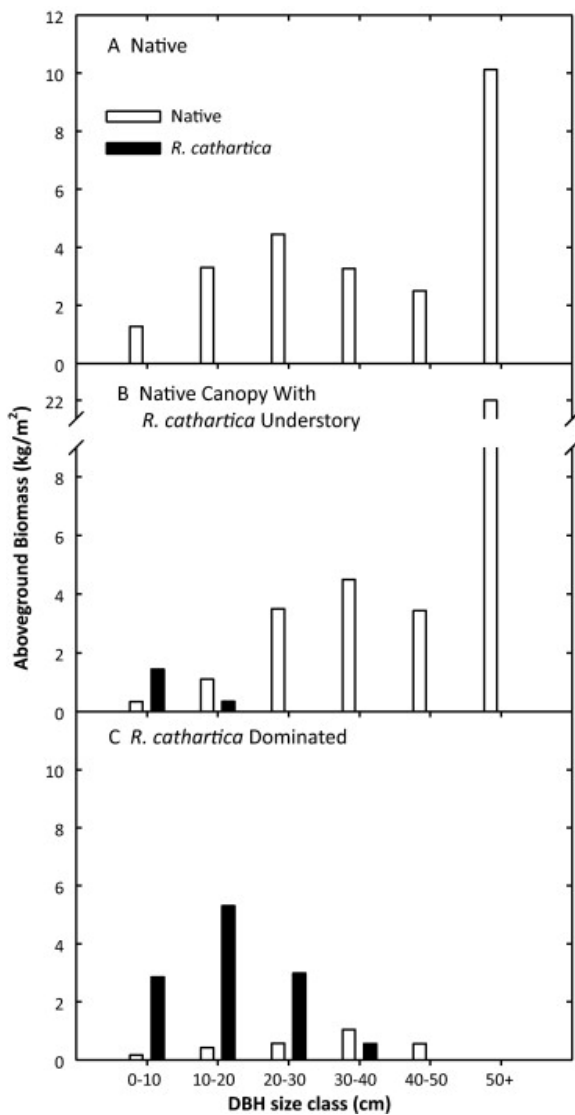
Fig. 2. Forest structure and mean biomass by 10-cm DBH size classes in (a) native-dominated sites with intact native understories (*n* = 8), (b) sites with native canopy but *Rhamnus cathartica* (common buckthorn) understories (*n* = 4), (c) sites dominated in the canopy by *R. cathartica* (*n* = 4).

Aboveground biomass increment was more than twice as high in native-dominated forests (including those with *R. cathartica* understories) than in forests dominated by *R. cathartica* (Mann–Whitney *U* test, *P* = 0.0029; Fig. 3). Between 2005 and 2008, we found that *R. cathartica* grew faster than other species at every diameter size class up to 10 cm, above which it grew slower than other species (Fig. 4).
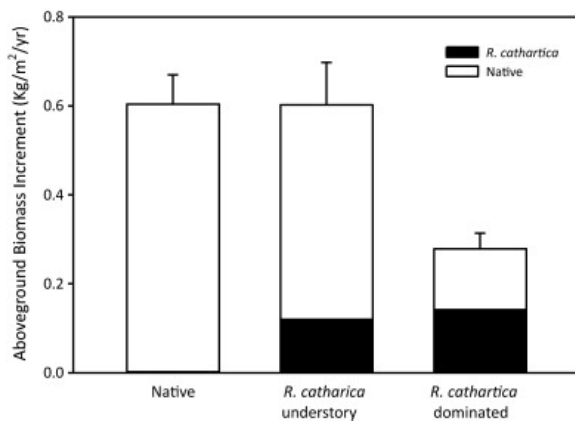
Fig. 3. Aboveground biomass increment (follows method 1, Clark et al., 2001) in native-dominated sites with intact native understories (n = 7), sites with native canopies and Rhamnus cathartica (common buckthorn) understories (n = 4), sites dominated in the canopy by R. cathartica (n = 4).
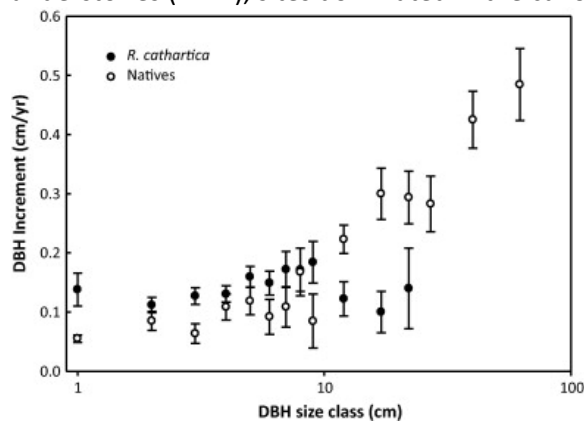

Fig. 4. Annualized growth of Rhamnus cathartica (common buckthorn) genets (n = 565) between 2005 and 2008 vs. all other species (n = 595 genets) according to DBH size class plotted on a log scale. Size classes are 1-cm DBH increments between 1 and 10 cm DBH, 5-cm increments between 10 and 30 cm DBH, and 20-cm increments thereafter. Error bars represent standard error on the mean in each size class.

4. Discussion

Introduced species can alter community composition and ecosystem structure, which in turn may change aboveground biomass storage and dynamics. We found that *R. cathartica*, which is commonly considered an understory shrub (Knight, 2005), can act as a forest canopy dominant (reaching heights of 13 m, Appendix 1), and that where such dominance occurs, aboveground biomass (of which ~48% is carbon) may be more limited relative to sites dominated by native tree species (Fig. 2). The disparity in aboveground biomass does not appear to be temporary or related to forest age. Although the *R. cathartica*-dominated stands are younger than most of the native-dominated stands, they are accumulating biomass more slowly (Fig. 3). In fact, the *R. cathartica*-dominated site with the highest aboveground biomass (24 kg/m^2) had a lower aboveground biomass increment (0.27 kg/m^2/year) than all the native-dominated sites (range 0.36–0.81 kg/m^2/year). This site may represent a near maximum biomass for *R. cathartica*-dominated forest. Aerial photographs and growth rings suggest that it has been dominated by *R. cathartica* since the 1960s (Mascaro and Schnitzer, 2007); many of the individuals are at or near their maximum size and have toppled and coppiced heavily, suggesting they may be suffering age- or size-related senescence.

There are two primary pathways by which *R. cathartica* could reduce aboveground carbon stocks in temperate forests: (1) by colonizing open sites and arresting succession in sites that would otherwise return to dominance by large native trees, or (2) colonizing the understory and replacing native canopy trees as they senesce. Our

results support the first pathway. In an analysis of land-use history at our sites, we found that our *R. cathartica*-dominated sites likely result from initial dominance by *R. cathartica* upon agricultural abandonment ([Mascaro and Schnitzer, 2007](#)). Over approximately 50 years, native canopy trees have not been able to attain dominance, suggesting that *R. cathartica* can arrest succession (e.g., [Niering and Goodwin, 1974](#)), thus preventing native canopy tree establishment and limiting biomass stocks in areas that would have otherwise undergone succession to native-dominated forest. Other studies also suggest that *R. cathartica* limits native tree establishment and growth ([Wyckoff et al., 2005](#), [Knight et al., 2007](#)). Compared to native species, *R. cathartica* growth rates were higher at small size-classes, but lower at size-classes larger than 10 cm DBH ([Fig. 4](#)). This suggests that initial colonization by *R. cathartica* may temporarily increase standing aboveground biomass more quickly than native species might, but that *R. cathartica* stands will saturate at lower maximum biomass levels than native forest.

With continued monitoring, we can determine whether *R. cathartica* will attain canopy dominance following understory colonization of intact forest (i.e., in sites where it is highly abundant in the understory, [Fig. 2](#)b). *R. cathartica* has a number of competitive advantages over native tree species, including extremely high shade tolerance, early and late-season growth when natives are dormant, and a facilitative relationship with introduced earthworm species that may increase nutrient availability ([Harrington et al., 1989a](#), [Knight et al., 2007](#)). Across Southern Wisconsin, *R. cathartica* has increased in abundance considerably since the 1950s ([Rogers et al., 2008](#)). Because of intrinsic size limitations, it is clear that replacement of large, high-biomass temperate trees such as *Quercus* spp. (oaks), *Acer* spp. (maples), and *Populus* spp. (cottonwoods) by *R. cathartica* at the landscape scale would result in a substantial decline in aboveground biomass.

Just as intrinsic size limitations on *R. cathartica* individuals can explain its effects on biomass, other introduced species affect biomass and forest structure based on their structural characteristics. For instance, the fynbos scrub biome in South Africa is widely invaded by introduced tree species, including *Acacia* spp., *Eucalyptus* spp., and *Pinus* spp., which increase aboveground biomass stocks three times above historical levels ([Milton and Siegfried, 1981](#), [Versfeld and van Wilgen, 1986](#)). A similar effect occurs on young Hawaiian lava flows that are colonized by *F. moluccana*, a N_2-fixing tree capable of increasing biomass stocks five-fold ([Hughes and Denslow, 2005](#)). Conversely, the small tree *P. cattleianum* (strawberry guava) causes biomass stocks to decline when it attains dominance in Hawai'i ([Asner et al., 2008](#)). Like *R. cathartica*, *P. cattleianum* has incredibly high growth rates when young, but is intrinsically limited in size, very rarely exceeding 30 cm DBH ([Wagner et al., 1999](#)). Structure in forests dominated by *P. cattleianum* mirrors that of forests dominated by *R. cathartica*: stands lack large trees, have low canopy height and less structural complexity, and have most biomass stored in smaller size classes ([Asner et al., 2008](#)). The formation of dense thickets of introduced shrubs and trees such as *R. cathartica* and *P. cattleianum* is increasingly common worldwide, and may lead to biomass declines if residual native canopies senesce ([Royo and Carson, 2006](#)). Introduced trees may also have a neutral effect on biomass. In Puerto Rico, a diverse complement of introduced species dominates large areas of forest that are comparable to native forests in their structural complexity and biomass stocks ([Lugo, 2004](#)).

Our results underscore the importance of species traits in influencing biomass stocks and forest structure. We found that where *R. cathartica* acts as a canopy dominant, aboveground biomass will be stored primarily in smaller trees and biomass increment will lower; and as a consequence, biomass will be more limited than in native-dominated forests.

Acknowledgements

Appendix A. Appendix 1

Attributes of 15 *Rhamnus cathartica* L. (common buckthorn) individuals harvested for allometry calculations.

Individual	DBH (cm)	Ground diameter (cm)	Height (m)	Aboveground biomass (kg)	Leaf biomass (kg)	Fruit biomass (g)
1	1.2	1.9	2.9	0.26	0.0229	–
2	1.4	2.0	3.4	0.38	0.0624	1.90
3	2.0	2.6	4.5	0.74	0.0867	–
4	2.8	4.1	4.9	2.02	0.2537	16.30
5	3.4	5.0	5.3	2.43	0.1983	–
6	3.6	5.1	4.2	2.74	0.1025	–
7	5.0	6.5	8.0	8.45	0.6396	–
8	6.5	8.5	7.5	13.90	0.7031	57.90
9	8.2	10.7	7.8	19.81	0.9909	–
10	11.4	15.5	7.3	41.98	2.3565	–
11	14.0	15.8	11.0	70.88	1.1194	232.90
12	18.2	25.9	12.0	150.28	4.1904	871.85
13	19.9	24.9	12.0	175.80	2.7617	–
14	22.5	25.4	9.5	194.09	3.7742	–
15	24.7	30.2	13.0	230.14	4.0554	–

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