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Treefall gaps required for establishment, but not survival, of invasive *Rubus phoenicolasius* in deciduous forest, Maryland, USA

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Abstract

Although plant invasions are often associated with disturbance, localized disturbances can promote invasion either by: (i) creating sites where individuals establish; or (ii) enabling an invader to colonize the entire stand. The former is expected when both establishment and survival to reproductive age require disturbed conditions, whereas the latter should occur in systems when either establishment or survival are limited to disturbed sites. We investigated the role of localized disturbance, specifically treefalls, in the invasion of the Asian Rubus phoenicolasius in a deciduous forest in Maryland, USA. We investigated the density and demography of R. phoenicolasius in treefall gaps of various sizes, but identical age to non-gap areas, using Classification and Regression Tree (CART) analyses to identify the most important predictors. To explore how the demography of established individuals responds to disturbed versus undisturbed conditions, we carried out a garden experiment with three different levels of shade (5, 12 and 22% full sun). We found vegetative and sexual reproduction, and seedling establishment, to be limited to large gaps in an old stand, but not in a stand in an earlier age of succession. However, in the garden experiment, established plants were able to survive and grow under all shade treatments. These findings indicate that R. phoenicolasius requires disturbances such as treefalls to establish in forests, but established plants will survive canopy closure, leading to stand-wide invasion. Managers should be able to prevent invasion, however, by inspecting large gaps for new recruits every 3 years.

Keywords: classification and regression tree analysis, invasive non-native plants, recruitment, *Rubus phoenicolasius*, seedling establishment, shade tolerance.

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Introduction

Understanding the mechanisms that enable exotic species to invade native communities is a topic of great contemporary interest (Williamson 1996; Lonsdale 1999; Belote *et al.* 2008; Eschtruth & Battles 2009), and informs two of the key research questions essential to reducing the impact of invasive species (Byers *et al.* 2002): 'what limits

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(Elton 1958; Hobbs & Huenneke 1992; Hutchinson & Vankat 1997; Daehler 2003; Huston 2004; Huebner & Tobin 2006; Chambers *et al.* 2007; DeGasperis & Motzkin 2007; Eschtruth & Battles 2009). This 'disturbance hypothesis' can be considered to be a subset of the resource enrichment hypothesis, that is, a community is invasible following an increase in unused resources (Davis *et al.* 2000; also Sher & Hyatt 1999). For systems characterized by localized disturbances (e.g. treefall gaps) as opposed to

the spread of non-indigenous species?' and 'what determines vulnerability to invasion in particular habitats?'

For invasive plants, there is extensive evidence that disturbance enhances the invasibility of communities (Elton 1958; Hobbs & Huenneke 1992; Hutchinson &

stand-wide disturbances, we distinguish two mechanisms (hypotheses) by which disturbance can promote invasion. First, localized disturbances can create sites where individuals of the invasive species can colonize, but do not become pervasive throughout the stand. Alternatively, localized disturbance can enable the invader to pervade the entire stand, although this may require several generations. If both establishment and survival are limited to disturbed sites, then the invader should remain a minor component of the community, not significantly influencing patterns of diversity or ecosystem function. However, if either establishment or survival occurs in the absence of new disturbances, then the extent and consequences of the invasion will increase as the species spreads.

Although climate and habitat models are useful for predicting the geographic range of an invasive plant (e.g. Thuiller et al. 2005; Ibañez et al. 2009), predicting the potential density or spatial pattern of an invader within suitable habitat in a new range cannot be inferred from static distribution data unless supplemented with temporal data. For example, where an invasive species is found only in recently disturbed sites, the invasion may continue to be limited to new disturbances, or these may initiate a more extensive invasion of the stand. Conversely, an invasive species that currently occurs throughout a stand might not be limited at all by disturbance, or it might require disturbance for establishment, but individuals then persist and spread by seeds or clonal growth as the site recovers. Thus, distinguishing the two hypotheses for how disturbance promotes invasion requires assessing: (i) whether establishment is limited to newly disturbed sites; and (ii) whether survival of established individuals is limited to newly disturbed sites. In the case of forest communities, the test is whether establishment or individual survival occurs under a closed canopy.

We tested these hypotheses in a deciduous forest where treefall gaps are the most prominent disturbance. Treefall gaps have multiple effects, for example, increased light penetration and below-ground resources, modified microclimate, reduced competition, and patches of bare mineral soil (Denslow 1987; Webb 1999); any one of these could enhance the germination and recruitment of invasive plants. We evaluated the role of disturbance on sexual and vegetative reproduction through comparisons of gap and non-gap plots, and the effect of post-disturbance conditions on survival and growth with a garden experiment.

Materials and methods

Study species

Rubus phoenicolasius Maxim (Rosaceae), wine raspberry or wineberry, is a raspberry native to Japan, China and Korea. It was introduced into the USA in 1890 as breeding

stock for new raspberry and blackberry cultivars, but escaped from cultivation and is listed as invasive in Maryland, Pennsylvania, Tennessee, Virginia, North Carolina and West Virginia (Spencer 2002). It is considered invasive by numerous federal and state agencies (Innis 2005). According to Swearingen *et al.* (2002) it 'occurs along forest, field, stream and wetland edges and in open woods, preferring moist habitats'. Compared to a co-occurring native congener, *Rubus argutus*, *R. phoenicolasius* had greater negative effects on a common forest herb, higher leaf nitrogen concentrations (N_{leaf}), greater specific leaf area (SLA) and higher maximal rates of photosynthesis (A_{max}) for a given dark respiration rate (R_d) (Innis 2005).

Growth and development of R. phoenicolasius follows that typical for Rubus. Seeds germinate in the spring and seedlings have a single stem. One-year-old plants either show continued growth of this stem or produce a new stem. Older plants produce stems that live for 2 years; in the first year they are unbranched 'primocanes'; in the second year they are woody 'floricanes' that produce branches and potentially flowers and fruits, but do not have extension growth. In our R. phoenicolasius populations individuals typically produced only one primocane per year, except under highly illuminated conditions. Short primocanes and floricanes are initially erect, but as they become longer they begin to arch. When arched canes touch the ground at the tip adventitious roots form (layering or tip-rooting), giving rise to new ramets (Imanishi et al. 2008). For reproductive floricanes, flowers are open in June and fruits mature in July. Pollination is primarily autogamous (Innis 2005), with most flowers setting fruit.

Study site

We compared the presence, density, size and growth of *R*. phoenicolasius in treefall gaps with that in randomly selected points in a deciduous forest at the Smithsonian Environmental Research Center ([SERC] 38°53'N, 76°33'W), Maryland (Parker et al. 1989). Although gap age is often confounded with gap size, because gaps decline in size as they age owing to in-growth of canopy trees bordering the gap and recruitment of advance regeneration into the canopy, we avoided this problem by selecting 22 gaps of uniform age, but a range of sizes. The gaps, formed during a severe storm on 5 June 2002, were located in a 46.5 ha portion of the SERC property in which approximately 9800 trees had been mapped (http:// www.serc.si.edu/labs/forest_ecology/big_tree.aspx). Twenty of the gaps were in a portion of the site dominated by a mature (~150-year-old) stand comprised largely of Liriodendron tulipifera, Quercus spp., Carya spp., Fagus gran-

difolia and Liquidambar styraciflua (Parker et al. 1989;



Fig. 1 Number of gaps grouped by damage category of focal tree, stand and size of the expanded gap (sensu Runkle 1982). 'Small' gaps were <200 m² and 'large' gaps were >290 m².

Kitamura *et al.* 2008), and two were in an adjacent young (~45-year-old) *L. tulipifera*-dominated stand.

Treefall gap and non-gap sites

In July 2004 we located 22 of the mapped trees that had been damaged in the 2002 storm. All of the gaps met the following criteria: they were upland sites, they were >20 m from forest edges or roads, they had not occurred within a pre-existing gap, and they had not expanded subsequent to the 2002 storm.

Each gap was classified by the damage caused to the focal tree (uprooted, snapped or topped), and its expanded gap area (sensu Runkle 1982; hereafter 'gap area') was calculated from the polygon formed by the bases of the live canopy trees that bordered the gap. For some descriptive summaries we distinguished 'small' gaps $(38-200 \text{ m}^2)$ from 'large' gaps $(290-959 \text{ m}^2)$ (Fig. 1). Within each gap we marked a 15 m × 15 m plot centered on the midpoint of the long axis of the gap (these extended beyond the gap area of the 'small' gaps). In addition, in two of the gaps formed by uprooted trees we also marked a second 15 m × 15 m plot that included the tip-up mound and pit, resulting in a total of 24 'gap' plots.

We also established $15 \text{ m} \times 15 \text{ m}$ 'non-gap' plots (*N* = 24) centered on points randomly selected from among all corners of a pre-existing 50 m × 50 m grid that met the first two criteria listed above (i.e. upland and > 20 m from edges or road). Although some of these

points were near small gaps, none were within gaps. Five of the non-gap plots were in the young stand and 19 were in the old stand.

Demographic measures

From 24 August to 24 September 2004 we tagged, counted and measured R. phoenicolasius seedlings and ramets in each plot. The stem length and number of leaves were recorded for all seedlings, which were operationally defined as individuals with just a solitary primocane <10-cm long with small leaves comparable to those of known seedlings. We recognize that some of these may have been small 1-year-old plants. The sizebased decision for classifying seedlings was based on an inspection of greenhouse-grown individuals of known age. For non-seedlings, stems were considered part of the same ramet if they originated from the same belowground organ (root + rhizome), or were within 10 cm of each other (excavation of several plants revealed that stems from the same rhizome were within 10 cm of each other). If the number of ramets in a plot exceeded 30, a random sample of 20 was selected; otherwise all ramets were measured. Measurements included the number of floricanes and primocanes, the length and number of branches and leaves on each, and the nature of the stem tip (aerial, did not touch the ground; prostrate, touched the ground, but was not rooted; rooted, touched the ground and was rooted). The number of fruits on each

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floricane was inferred from the number of calyces. The presence of the previous year's floricane was also noted.

Plots were recensused between 1 and 23 June 2005; seedlings and ramets were measured as in 2004 to determine seedling and ramet growth and survival, and new recruitment of seedlings. Plots were again recensused between 16 and 20 July 2006 to determine survival and, for seedlings only, growth. Between 29 June and 6 July 2007 we again recensused seedlings in the old stand; the young stand had been disturbed by logging.

Environmental parameters

The light environment of each plot was quantified by the instantaneous percentage photosynthetic photon flux density (%PPFD), which was obtained by dividing the understory PPFD by simultaneous measurements above the canopy (Messier & Puttonen 1995). This method explained 88% of the variation in the long-term integrated percentage PPFD (Machado & Reich 1999) and was the best predictor of PPFD over the growing season (Gendron et al. 1998). We measured photosynthetically active radiation (PAR) for 2 min at five points in each plot (center and 5 m in each cardinal direction) using a Li-Cor LI-1000 quantum sensor and datalogger (Lincoln, NE, USA). Measurements were made on overcast days between 20 June and 29 July 2005 and divided by the average PAR data monitored at the SERC dock for the same 15-min time periods (C. Gallegos, unpubl. data, 2005).

To investigate the importance of litter on invasibility, we sampled 25 points in each plot (every 3 m on a 12 m \times 12 m grid centered on the plot center) in July 2006. At each point we dropped a chaining pin and counted the number of leaf layers (number of leaves or recognizable leaf fragments) pierced by the pin. If no leaf litter was encountered, we scored whether the point was on bare ground, duff, coarse woody debris, or other ground cover. We calculated for each plot the proportion of points with bare ground (hereafter '%bare') and mean litter depth.

Statistical analyses

To understand what environmental parameters best explain the presence and density of *R. phoenicolasius* ramets among stands, as well as seedling density and survival and fruit production, we used a classification and regression tree analysis ([CART] Breiman *et al.* 1984; De'ath & Fabricius 2000; Prasad *et al.* 2006). A CART analysis is an approach that can be used to explain the variation in a response with explanatory variables that accommodate non-linear and higher-order interactions; CART analyses are increasingly being used for complex ecological data (De'ath & Fabricius 2000). The CART analysis and other tree-structured methods are particularly useful in exploratory studies because of the simplicity of their resulting models. The results can be interpreted as a series of decision rules, highlighting the most important explanatory variables in an intuitive manner and omitting those that are less relevant. Moreover, these models are flexible and predominantly non-parametric: they do not rely on distributional assumptions for the underlying data, and their interpretation is not limited by the formality of hypothesis testing. Models for categorical dependent variables are called classification trees, and models for quantitative dependent variables are called regression trees.

To model a quantitative response, a regression tree is constructed by iteratively splitting the data based on simple decision rules, each of which involves an individual explanatory variable. Each resulting subgroup of the data is assigned a constant predicted value: the subgroup's mean response. To determine the appropriate splitting rules, a goodness-of-fit criterion (e.g. sum of squared errors) is evaluated at each step. For example, suppose we were modeling primocane length as a function of gap length and other variables. The CART analysis would consider every possible split of the form 'is gap length $\leq c$?' and evaluate the goodness of fit for each resulting model. Every possible split on each remaining variable would be similarly evaluated. The decision rule that is ultimately chosen optimizes the goodness-of-fit criterion. The process is then repeated on each resulting subgroup and iterates until no further splits are possible. A similar procedure, adjusted for categorical responses, is used to build a classification tree. Of course, a tree grown as far as possible will provide an excellent fit to the data in a particular sample, but its prediction rules may not generalize well to new observations. Therefore, trees are 'pruned' (i.e. the number of splits is reduced) so that the early splitting rules are retained, but splits based on very small subsets of the data are eliminated. This situation raises two questions: (i) how do we assess the 'fit' of a tree model in a way that has meaning outside our dataset; and (ii) how do we determine the optimal extent of pruning?

First, we must select a criterion on which to evaluate our model. For a classification tree, we examine the misclassification rate (MC), which describes the percentage of cases that our model incorrectly characterizes. This measure can range from 0 to 100%, with an error-free model having MC = 0%. For a regression tree, we use the root mean squared error (RMSE), which is essentially the standard deviation (SD) of our prediction errors. This measure can range from 0 to infinity, with an error-free model having RMSE = 0.

Typically, the MC or RMSE that is calculated for a particular model overstates the predictive accuracy of the model outside the dataset on which it was built. That is,

Dependent variable	Split descriptors	Plots with ramets (%)	Ν	CV MC rate (%)	Model-free MC rate (%)
Ramet presence (Fig. 2)		58.3	48	16.7	41.7
1 (0)	%PPFD >4.44	90.9	11		
	%PPFD ≤4.44				
	Old	13.3	30		
	Young	85.7	7		

Table 1 Summary of the classification tree model results

The dependent variable and its overall summary statistics are presented in italics. CV MC rate, the cross-validation estimate of the out-of-sample misclassification rate; Model-free MC rate, the misclassification rate implied with no model (i.e. a root node only, no splits); %PPFD, the percentage of open sky photosynthetically active radiation.

in-sample MC and RMSE tend to be lower than out-ofsample MC and RMSE. To estimate the out-of-sample MC or RMSE of a model and simultaneously determine the optimal extent of pruning, we use leave-one-out crossvalidation and the 0-SE rule (Breiman *et al.* 1984).

The leave-one-out cross-validation procedure with a dataset of N observations proceeds as follows. For each observation k from 1 to N, fully grow a tree based on the entire dataset excluding observation k. Consider a nested sequence of trees of different sizes (e.g. one split, two splits) that represents various levels of pruning on the fully grown tree. Use each of these models to predict observation *k* and record the prediction errors. At the end of these N steps, compute the resulting MC or RMSE for each tree size. As these computations are based on out-ofsample predictions, they provide information about the ability of the models of various sizes to generalize to new observations. To select our final classification or regression tree model, we select our tree size based on the 0-SE rule: select the tree size that minimizes the out-of-sample MC or RMSE criterion. As the out-of-sample estimate of predictive accuracy was selected based on cross-validation, we refer to it as CV MC or CV RMSE.

To aid our interpretation of these values for each of our models, we report them alongside the model-free MC and model-free RMSE in Tables 1 and 2, respectively. The model-free MC for a categorical dependent variable uses the most common class as the predicted class for all cases in the sample. For example, in Table 1, 58.3% of the plots have ramets and 41.7% do not. A model-free predictor would guess that all plots have ramets, resulting in a model-free MC of 41.7%. The model-free RMSE for a quantitative dependent variable uses the (weighted) sample mean of the dependent variable as the predicted value for all cases. Therefore, the RMSE is simply the (weighted) sample SD of the dependent variable. Comparing the CV MC to the model-free MC (or the CV RMSE to the model-free RMSE) can provide a crude indication of the explanatory power of a tree-based model.

In the present study, unless otherwise noted, the explanatory variables included in each model were: stand

(young, old), plot type (gap, non-gap), gap type (uprooted, snapped, topped or not a gap), %PPFD, litter depth, gap length and gap area. For non-gap plots, gap length and area were set at 0. All CART analyses, except seedling analyses, were carried out in software commercially available from Salford Systems (San Diego, CA, USA). Each tree is represented graphically, with the 'root node' (undivided data) at the top and with each split dividing the data into two groups (represented as nodes) based on the univariate rule. We used a classification tree for the categorical variable of ramet presence/absence in 2004.

For those plots with at least one ramet in 2004, we used regression tree analyses to examine ramet density (number of ramets per plot in 2004), primocane size (mean cane length and mean number of leaves in 2004, each weighted by ramet density) and the number of fruits per ramet (separately for 2004 and 2005, both with and without weighting by the number of floricanes, omitting litter depth from the list of explanatory variables).

To analyze seedling density, we combined plants scored as seedlings in 2004 (N = 94) with new seedlings first censused in 2005 (N = 72) because the patterns were qualitatively similar. This combined number of seedlings per plot was analyzed using a piecewise-constant Poisson regression tree (Chaudhuri *et al.* 1995) in GUIDE software (Loh 2002).

First-year survival of seedlings was analyzed at the plot level. We calculated, separately for the 2004 and 2005 cohorts, the proportion of seedlings in each plot that survived, and then analyzed each with a regression tree analysis. In each analysis, the survival proportion was weighted by the number of seedlings.

To test whether old and young stands differed in %bare or mean litter depth we used a one-way MANOVA between groups design using SAS PROC GLM (Cary, NC, USA).

Garden experiment

To experimentally determine the effect of canopy closure on seedling and ramet survival, we simulated different light environments in 12 shade structures (each approxi-

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Dependent variable	Split descriptors	Avg	Ν	W	CV RMSE	Model-free RMSE
Primocane length (Fig. 3)	109	20		36.1	38.5
0 . 0 .	Gap length ≤ 26 m	73	13	9.0		
	Gap length > 26 m	139	7	11.0		
No. fruits per ramet 2004		1.3	20		1.17	1.52
1	$\%$ PPFD ≤ 4.4	0.4	10	9.0		
	%PPFD > 4.4					
	Young	4.3	1	3.5		
	Old					
	Gap length \leq 35.6 m	1.4	6	5.6		
	Gap length > 35.6 m	0.0	3	1.9		
No. fruits per ramet 2005 (Fig. 5)		2.0	22		0.28	0.97
-	Gap area $\leq 437 \text{ m}^2$	0.8	16			
	Gap area > 437 m^2	5.1	6			
No. seedlings (Fig. 6)		3.5	48		1.51	8.31
	Gap area $\leq 153 \text{ m}^2$	0.7	33			
	Gap area > 153 m^2	9.6	15			
First-year seedling survival 2004		67%	16		16.2%	30.2%
	$\%$ PPFD ≤ 4.93	87%	9	8.0		
	%PPFD > 4.93	47%	7	8.0		
Seedling survival 2005 (Fig. 7)		46%	15		22.4%	26.0%
-	Layers ≤ 1.5	89%	5	1.9		
	Layers > 1.5					
	Gap length > 21 m	54%	3	4.6		
	Gap length ≤ 21 m					
	Gap area $\leq 128 \text{ m}^2$	67%	3	0.6		
	Gap area > 128 m ²	29%	4	7.9		

Each dependent variable and its overall summary statistics are presented in italics, along with the figure where the corresponding regression tree is illustrated. Avg, the (weighted, where applicable) average of the dependent variable; N, the actual number of observations; W, the effective number of observations after weighting; Layers, the average number of leaf litter layers in a plot; %PPFD, the percentage of open sky photosynthetically active radiation; RMSE, the estimated root mean squared error of prediction for out-of-sample observations. The model-free RMSE is simply the sample standard deviation.

mately $1.2 \text{ m} \times 1.2 \text{ m} \times 0.6 \text{ m}$) in an experimental garden at SERC. Grades of black shade cloth were used to achieve conditions of 5–5.5, 12 and 22% full sun (based on 12-h light measurements made inside each shade structure in May 2006). These treatments hereafter are referred to as 'low', 'medium' and 'high' light. The light levels were selected to approximate conditions measured in closed canopy, new gaps and forest edges in the study area. Each light treatment was represented as one enclosure in each of four blocks; each block was sheltered from the rain with 4 mm 'Film-Gard' polyethylene (Carlisle Plastics, Minneapolis, MN, USA). In each enclosure we placed one pot with seeds to quantify seedling emergence, six pots with 1-year-old plants and six pots with '2-year-old' plants to quantify survival and growth.

Seedling emergence

Seeds for the seedling emergence pots were obtained from fruits collected on 7–8 July 2004, stored at 4°C, scarified with sulfuric acid and rinsed with calcium hypochlorite (as per Swartz (2002)) on 31 January 2005, and then sown on flats in a mixture of paver sand and PRO-MIX GSX. On 1 February these flats were placed in beds in the experimental garden and covered with *Liquidambar styraciflua* leaves and snow for 'cold stratification' for the duration of the winter. On 3 May the sand and PRO-MIX mixture containing the stratified seeds was well mixed and an equal volume (100 mL) was placed on top of each of 12 15 cm (width) standard pots (14 cm deep, 1750 cc capacity) filled with a 1:1 mixture of paver sand and PRO-MIX GSX (mixture pH 6.7–7.0).

Counts of emerged seedlings were made approximately monthly from 31 May to 17 August, and again on 6 October 2005. For each pot we determined the maximum number of seedlings observed at any census, and tested for any treatment effects using a one-way ANOVA.

Growth of established genets

One-year-old plants had germinated in the greenhouse in May–June 2004 from seeds collected in 2003 and scarified

in December 2003 using the procedures described above. 'Two-year-old' plants had germinated in the greenhouse during October 2003 from seeds collected in 2003. Individuals of both cohorts were transplanted into 15 cm (1-year-old plants) or 22 cm (2-year-old plants) clay pots that were filled with a 1:1 mixture of paver sand and PRO-MIX GSX. To provide an inoculum of mycorrhizal fungi, a 50 mL slurry of soil collected from an established stand of R. phoenicolasius at SERC was added to all but the seedling pots. Pots were placed into beds in the experimental garden where they were covered with two sheets of foam between 13 December 2004 and 14 March 2005. The uncovered pots were placed into the shade structures on 25 April 2005. The pots were assigned to blocks and treatments on a stratified random basis; two size classes of 1-year-olds and three size classes of 2-year-olds were recognized, and equal numbers of each were assigned to each enclosure. Water was provided ad libitum approximately weekly. Fertilizer was applied on 18 August 2005 in the form of Osmocote 19-6-12 slow-release (4-month) pellets (5 g per 15 cm pot and 10 g per 22 cm pot).

On 6 October 2005 the plants were removed from the shade structures and end-of-season measurements were made. At this time all floricanes had senesced, but primocanes were only beginning to senesce. The larger two of the three size classes of 2-year-old canes were harvested and separated into primocane leaves, primocane stems (canes and branches) and below-ground organs (roots plus stolon). The area of all primocane leaves was determined using a tabletop Li 3100 leaf area meter (Lincoln, NE, USA). All parts were dried at 60°C until the weight was constant. Most material was weighed on a Sartorius MC1 balance (Goettingen, Germany), except for the roots and very small items, which were weighed on a Mettler AE160 electronic balance (Mettler-Toledo, Columbus, OH, USA). Leaf area was divided by leaf mass to obtain the specific leaf area (cm^2/g) .

Relative growth rates (RGR) of plants were estimated using non-destructive measures. For 1-year-old plants we calculated leaf RGR as:

$$RGR_{L} = [ln(L_{t2}) - ln(L_{t1})]/(t_{2} - t_{1})$$

where L_{t2} is the number of leaves on primocane(s) at the end of the growing season (t₂, October 2005) and L_{t1} is the number of leaves on the primocane at the beginning of the growing season (t₁, April 2005).

For 2-year-old plants we calculated stem (canelength) RGR as:

$$RGR_{C} = [ln(C_{t2}) - ln(C_{t1})]/(t_{2} - t_{1})$$

where C_{t2} is the summed lengths of the primocanes in October 2005 (t₂) and C_{t1} is the length of the floricane, including major branches, in April 2005 (t₁).

The effect of the light treatment on each parameter was initially evaluated with a one-way ANOVA with shade structure (N = 12) nested in treatment. Because the nested factor was not significant in any analysis it was dropped from the statistical model, and the effects of the light treatments were evaluated using simple one-way ANOVAS; when treatment was significant, pairwise comparisons of least square means were made using a Tukey's adjustment for multiple comparisons in SAS PROC GLM.

Results

Presence of R. phoenicolasius

The optimal classification tree for the presence versus absence of ramets in 2004 had two splits, resulting in three terminal nodes. Plots were first split by light, with *R. phoenicolasius* present in 10 of the 11 plots with >4.44%PPFD, but in only 10 of the 37 plots with \leq 4.44%PPFD (Table 1; Fig. 2). Those plots with lower light availability were split again; *R. phoenicolasius* was absent in 86.7% of the old stand plots, but present in 85.7% of the young stand plots. The pattern was similar in 2005, except the first bifurcation was dependent on gap size rather than light availability (results not shown).

Ramet density

Among the plots where ramets were present, the number of ramets per plot was not explained by the measured variables (i.e. the optimal regression tree had no split).

Ramet size

Both measures of 2004 primocane size (cane length and number of leaves) were significantly affected by gap size. The optimal regression tree for primocane length split the seven plots in the longest gaps (gap length >26 m), where primocanes averaged 139 cm, from the 13 plots with gap length <26 m (including non-gap plots), where primocanes averaged 73 cm (Table 2; Fig. 3). The optimal regression tree for the number of leaves on primocanes had two splits: the first split plots in the eight largest gaps (gap area >380 m²), where primocanes averaged 11 leaves (results not shown). The large gap group was next split by litter depth: in the one plot with litter depth < 1.0 layers primocanes had more leaves than in the seven plots with deeper litter.

Ramet survival

Most ramets recorded in 2004 were still alive in 2005 and 2006. Even in plots with low light, survival of ramets was



Fig. 2 Optimal classification tree for the presence ('TRUE') versus absence ('FALSE') of ramets of *Rubus phoenicolasius* in 48 plots, each $15 \text{ m} \times 15 \text{ m}$. %PPFD, the percentage of open sky photosynthetically active radiation; AGE, signifies old or young stand.



Fig. 3 Optimal regression tree for mean primocane length of *Rubus phoenicolasius* ramets. The plot means were weighted by the number of ramets. N, the actual number of observations in a node; W, the weighted number of observations; GAPLEN, the length of the expanded gap in meters; plots not in gaps are included in Terminal Node 1.

high. For example, in plot R9 in the young stand, all seven ramets recorded in 2004 were still alive in 2006. Plot R20 in the old stand had only two ramets, each consisting of just a single primocane, in 2004; in 2005 both of these were alive and each had both a primocane and a floricane, but both were dead in 2006.

Vegetative reproduction

Longer primocanes were arched, and those that exceeded 1 m in length frequently touched the ground and were tip-rooted. Tip-rooting was common among canes \geq 1 m (48% of primocanes, 26% of floricanes); presumably the floricanes had tip-rooted the previous year, when they were primocanes. Tip-rooting was never observed for canes <1 m, which comprised the majority of both age classes. Because large gaps had the longest canes, tip-rooting was frequent (Fig. 4), whereas in small gap and non-gap plots tip-rooting was extremely rare. The rooted



Fig. 4 Proportion of *Rubus phoenicolasius* primocanes and floricanes that were rooted at the tip in August/September 2004 in non-gap, small gap and large gap plots. Sample sizes (primocanes, floricanes) are non-gap (37, 33), small gap (16, 9) and large gap (169, 69).

tips nearly always were the source of new primocanes, sometimes during the same growing season, but more commonly in the next growing season. Subsequently, new ramets grew from these rooted tips; tip-rooting was the predominant form of vegetative reproduction in *R. phoenicolasius*. Ramets produced by tip-rooting were typically approximately 1 m from the base of the parent ramets.

Sexual reproduction

In 2004 in the old stand, fruits were present in three large gap plots, but no small gap or non-gap plots. In the young stand, fruits were found in all gaps, but in only one nongap plot. Among plots with *R. phoenicolasius*, the number of fruits per ramet in 2004 was best explained by a regression tree with three splits when this variable was weighted by the number of floricanes (Table 2). The first node split plots with >4.4%PPFD (which averaged 2.1 fruits per ramet) from plots <4.4%PPFD, which averaged only 0.4 fruits per ramet. Among those higher light plots, the second node split the single non-gap plot in the young stand, which averaged 4.3 fruits per ramet, from the nine plots in gaps in the old stand, which averaged 1.0 fruit per ramet. Among those old stand plots in gaps, the third node split plots based on gap length: no fruits were produced in longer gaps. If fruits per ramet was not weighted, there was no optimal tree.

A similar pattern was found in 2005: in the old stand fruits were present in five large gap plots, but no small gap or non-gap plots; in the young stand fruits were



Fig. 5 Optimal regression tree for the number of fruits per ramet unweighted on the 22 plots with *Rubus phoenicolasius* present in 2005.



Fig. 6 GUIDE piecewise constant Poisson regression tree model for *Rubus phoenicolasius* seedlings (combined number of seedlings first censused in 2004 and 2005). GAPAREA, expanded gap area in m²; plots not in gaps are included in Terminal Node 1.

found in all four gaps and two of the five non-gap plots. When fruits per ramet was weighted by floricane number, there was no optimal tree (results not shown). However, when fruits per ramet was unweighted, the optimal regression tree had a single split: plots in the largest gaps (>437 m²) averaged 5.1 fruits per ramet compared with only 0.8 fruits per ramet in smaller gaps and non-gap plots (Table 2; Fig. 5).

Seedlings

Combining seedlings first censused in 2004 and 2005, the optimal Poisson regression tree split plots on the basis of gap area (Table 2; Fig. 6). The 15 plots with gap area >153 m² averaged 9.6 seedlings, whereas the remaining plots (nine smaller gaps and 24 non-gap plots) averaged 0.67 seedlings. Ten plots in the latter group had seedlings; of these, most were in the young stand (N = 4) or were small gaps in the old stand (N = 4). Two non-gap plots in the old stand had one seedling each in 2005, one of which survived to 2006.

Seedling survival

Although nearly all seedlings occurred in gaps, first-year survival of the 2004 cohort of seedlings was significantly



Fig. 7 Optimal regression tree for first-year survival of *Rubus phoenicolasius* seedlings established in 2005 weighted by the number of seedlings per plot. N, the actual number of observations in a node; W, the weighted number of observations; LAYERS, the average number of leaf litter layers in a plot.

higher in the young stand (100% of 20 seedlings) than in the old stand (58% of 74 seedlings; ANOVA of the plot data weighted by seedling number F = 10.82, P = 0.0054). Regression tree analysis of mean seedling survival among the 16 plots with seedlings in 2004 resulted in an optimal tree with a single split: survival was lower (47%) in plots with > 5% PPFD than in plots with <5% PPFD (87%) (results not shown). Second-year survival was 40% of 20 seedlings in the young stand and 58% of 43 seedlings in the old stand. Third-year survival, in the old stand, was 60% of 25 seedlings. Only one of these 3-year-old plants, in a large gap, was reproductive.

First-year survival of the 2005 cohort of seedlings was 60% (of 10) in the young stand versus 44% (of 62) in the old stand. The optimal regression tree for plot-level seedling survival, weighted by the number of 2005 seedlings, had three splits (Table 2; Fig. 7). The first node split plots that had >1.5 layers of leaf litter, where survival averaged 40%, from those with less deep litter, where survival averaged 89%. Among the first set of plots, those with gap length >21 m averaged higher seedling survival (54%) than those in smaller gaps or non-gaps, where survival averaged 32%. Second-year survival, assessed only in the old stand, was 67% of 27 seedlings; none were reproductive.

Differences between the young stand and the old stand

The MANOVA revealed a significant multivariate effect of stand age on litter characteristics (Wilks' lambda = 7.44, d.f. = 2, 38, P = 0.0019). Plots in the young stand (N = 9) averaged 0.9 (0.4, SD) layers of leaf litter and 12% (10%) bare ground compared with 1.7 (0.6) layers and 5% (6%) in the old stand (N = 32).

Garden experiment

Light levels The light levels reached in our garden plots were somewhat higher than the conditions they were intended to simulate, yet provided distinct light environments across an ecologically relevant scale. Our low light treatment (5-5.5% PPFD) was higher than our measurement of %PPFD in non-gap plots, which averaged 2.1% in the old stand and 2.0% in the young stand, similar to that reported for two plots in the old stand (2.5 and 2.3%) by Brown and Parker (1994). Our medium treatment (12% PPFD) was higher than our average values of 3.7 and 6.6% across small and large gaps, respectively, in the old stand in 2005, but light was undoubtedly much higher in 2002, when the gaps were formed. The high light treatment (22%) was comparable to the light environment in a R. phoenicolasius patch along a single lane road through the old stand (21.7%).

Seedling emergence Seedling emergence was complete by 30 June 2005 and was similar across the shade treatments (Table 3). Seedling mortality during the summer was low. Seedlings grew little during the growing season, less than seedlings grown in the greenhouse in previous years.

Growth of 1-year-old genets The RGR, based on the number of primocane leaves, was positive in all treatments, but differed significantly across treatments; plants in the high light treatment had significantly greater growth than those in the low light treatment (Fig. 8).

Growth of 2 year-old genets The RGR, based on cane length, was positive in all treatments, but differed significantly across treatments (ANOVA; F = 5.52, d.f. = 2, 69, P = 0.006), with medium light plants having a significantly greater increase in length than low light plants (Fig. 9). For harvested plants, the treatment significantly affected both primocane shoot biomass and root biomass, but not the root : shoot ratio (Table 3). Shoot biomass was significantly greater in high than in low light; root biomass was significantly greater in high than in low light, and intermediate at medium light. Primocane leaf area also differed across treatments, but in this case medium light plants had significantly greater values than high light plants (Table 3). Specific leaf area differed

Table 3 Mean parameters for *Rubus phoenicolasius* in each of the three light treatments in the garden experiment, with statistics for the one-way ANOVA on treatment

Parameter	High light	Medium light	Low light	F	Р
Seedlings per pot	9.75	9.00	5.00	0.78	0.4890
Shoot biomass (g)	6.23a	5.59a	3.67b	7.48	0.0021
Root biomass (g)	2.70a	1.99ab	1.36b	5.98	0.0061
Root : shoot ratio	0.43	0.35	0.36	1.76	0.1881
Leaf area (cm²)	961.76ab	1147.58a	672.54b	7.10	0.0027
Specific leaf area (cm²/g)	268.83b	338.60a	332.19a	4.99	0.0128

For seedlings per pot, there were four replicates per treatment, with df = 2, 9. All other parameters are based on 12 harvested 2-year-old plants per treatment, with df = 2, 33. There was no effect of shade structure nested within treatment, so this term was dropped from each ANOVA. Parameters differing significantly across treatments are highlighted in bold. Different letters indicate treatments that differed significantly in least square means based on Tukey's adjustments for multiple comparisons.



Fig. 8 Mean (+standard error) leaf relative growth rate (RGR) over one growing season of primocanes on 1-year-old *Rubus phoenicolasius* plants under different light treatments in the garden experiment. The RGR_L (relative growth rate for 1-year-old plants) differed significantly among treatments (ANOVA; *F* = 9.36, d.f. = 2, 54, *P* = 0.0003); different letters indicate treatments that differed significantly in RGR_L least square means based on Tukey's adjustments for multiple comparisons.

among treatments, with high light plants averaging significantly lower values than the other two treatments (Table 3).

Discussion

The findings of the present study indicate that treefall gaps are essential for the establishment of *R. phoenicolasius* in the old stand, but not in the young stand. However, established individuals are able to survive undisturbed conditions.

Evidence that gaps are required for the establishment of *R. phoenicolasius* includes our findings that the presence of established ramets was best predicted by light availability in 2004, and by gap size in 2005. However, among plots with lower light availability, ramets were much more



Fig. 9 Growth of 2-year-old *Rubus phoenicolasius* plants under the different light treatments in the garden experiment, illustrated as mean (+standard error) length of floricane(s) at the beginning of the growing season, and of primocanes at the end of the growing season. Different letters indicate treatments that differed significantly in RGR_C (relative growth rate for 2-year-old plants) least square means based on Tukey's adjustments for multiple comparisons.

likely to be found in the young stand than in the old stand. In addition, in the old forest, seedlings were almost entirely restricted to larger gaps. This pattern could result from restricted seed dispersal from adults fruiting in these gaps or directed dispersal of seeds to gaps by animals (Hoppes 1988). We argue that seedling establishment, rather than propagule pressure, is driving this pattern because plots associated with uprooted trees averaged twice as many seedlings as those associated with snapped or topped trees, or the crown zone of uprooted trees. It appears that disturbance to the litter layer (i.e. exposure of mineral soil), as well as high light, is needed for seedling establishment. Further evidence that canopy shade is not the critical factor in the suppression of seedling emergence came from the garden experiment, where emergence was independent of shade treatment, although it is possible that seedling shade tolerance is lower in the competitive environment of the forest. Within the gaps of uprooted trees, seedlings tended to be found on or near tip-up mounds and pits, supporting previous findings that bare soil promotes seedling establishment (Innis 2005). Deeper litter also reduced the survival of first-year seedlings of the 2005 cohort. The lower survival of seedlings of the 2004 cohort in higher light plots might have resulted from moisture stress at some critical point in the growing season.

Evidence that treefall gaps are essential for sexual reproduction in the old stand includes our finding that fruiting in the old stand occurred only in large gaps, and across stands fruits per ramet was best predicted by light availability in 2004 and gap size in 2005. We concluded that vegetative reproduction is dependent on gaps because tip-rooting occurred only in canes longer than 1 m, and only ramets in large gaps achieved these lengths.

However, survival and growth of established ramets was high, regardless of the light environment, indicating individuals will survive canopy closure and persist under closed canopy conditions. Although only a few ramets were found outside of gaps, they survived and grew, as did all ramets in the low-light treatment in the garden experiment. This low-light treatment did not reduce light levels to those typical of canopy sites, but the fact that all plants increased in size suggests they would have survived even greater shade. The greater specific leaf area exhibited by plants in the low-light and medium-light treatments is a classic developmental response of shade tolerance that has been observed in other forest invaders (Sanford et al. 2003). However, the root : shoot ratio did not respond to shade treatment, unlike the adaptive growth response of the invasive Acer platanoides to deep shade (Reinhart et al. 2006). Growth was greater in the higher light treatments, consistent with our field observation of greater density and size in higher light environments, and consistent with the idea that the light environment is critical for expansion and reproduction of R. phoenicolasius genets (Innis 2005). A native congener, Rubus idaeus, showed growth responses to higher light, but unlike wineberry it was not particularly shade tolerant (Ricard & Messier 1996).

Differences between the stands

Because relatively few plots were studied in the young stand, we had little power to assess whether demographic patterns differed from those in the old stand. However, some patterns were compelling. The young stand was characterized by higher seedling survival than the old stand, and was the only place where *R. phoenicolasius* fruited outside of gaps. Among plots with lower light levels, those in the young stand were significantly more likely to have established ramets, and had significantly more fruits per ramet in 2004, than their old stand counterparts. Thus, treefall gaps were not required for seedling establishment or sexual reproduction in the young stand.

The higher demographic rates of wineberry in the young stand were not likely to result from higher light, as non-gap plots in the young stand did not have higher %PPFD than those in the old stand, although it is possible that they differed in some other aspect of the light environment. Thus, it is likely that some factor other than light limits growth in the old stand, such as the level of root pathogens or a limiting nutrient. The experimental addition of phosphorus increased the density of the invasive R. argutus in wet forest in Hawaii (Ostertag & Verville 2002). Several of our findings point to litter as the critical factor causing the demographic differences between stands. The young stand averaged fewer layers of leaf litter, and a greater proportion of bare soil, than the old stand. Litter was the best predictor of survival of the 2005 cohort of seedlings, with lower survival on plots with more litter. Field experiments have revealed that litter inhibits seedling establishment of R. phoenicolasius (Innis 2005).

The shallower mid-summer litter depth in the young stand is not the result of a lower input of leaves during autumn leaf drop, because the stands have comparable levels of leaf area index (LAI) and litter-fall (J. Parker, pers. comm., 2005). Rather, it is likely to result from more rapid decomposition of leaves in the young stand. Although differences in litter composition may partly explain this difference (the young stand had more Liriodendron, with easily decomposable leaves, and less Fagus and Quercus, with recalcitrant leaves), ongoing studies in the same forest (M. McCormick, pers. comm., 2009) have shown that young stands have higher biomass of non-native earthworms and higher rates of litter decomposition in the same stands. These results suggest that higher rates of litter turnover result in increased incidences, both in space and time, of no litter or little litter cover, conditions that favor wineberry seedling establishment.

Conservation and management implications

The established paradigm of good news : bad news can be applied to the potential invasion of *R. phoenicolasius* in mature forest stands. The bad news is that this invasive will become pervasive even in old stands. Individuals that establish in treefall gaps can reproduce sexually and/or asexually before being slowed by canopy closure, and furthermore will survive canopy closure as established

ramets. It is also likely that their seeds will remain dormant in the seed bank, awaiting the next treefall gap, given the prevalence of dormancy in congeners such as *R*. idaeus (Whitney 1986). The good news is that the invasion of old stands can be prevented by simple cultural control. As seedling establishment is limited to gaps, only gaps need to be searched for R. phoenicolasius seedlings and young plants. Efforts can be focused on large gaps and gaps caused by uprooted trees because most seedlings were restricted to these sites. Because seedlings will not fruit or reach adequate size for tip-rooting for at least 3 years, even under the high light conditions of large gaps, removal of these small plants only once every 3 years will be sufficient to prevent invasion. A small team of technicians or volunteers trained to identify this species could efficiently prevent invasion of a large stand.

Similarly, patrol-detect-and-remove practices are likely to be effective against a large set of invasive plant species in ecosystems characterized by localized disturbance. Candidates for this control strategy are speciessite systems where establishment, but not survival, requires disturbance (disturbance-mediated stand invasion hypothesis). Within this category one would likely place the Prunus serotina invasion in deciduous forest in Belgium. Seedlings of this North American tree are restricted to high light areas of the forest floor, but saplings also occur in shade (Godefroid et al. 2005), indicating that once they establish, individuals can survive canopy closure. The Rubus alceifolius invasion in lowland tropical rain forest on Réunion also likely fits in this category, as seedlings only germinate in large gaps, but juveniles persist in shade (Baret et al. 2008). Although treefall gaps provide only a transient elevation of irradiance, this is apparently sufficient for rapid growth, and adults are strongly associated with gaps, particularly large gaps, the same pattern reported here for R. phoenicolasius. A combination of field observations and garden experiments, such as those described here, will be sufficient to identify which invasive plants, in which communities, can be controlled by this simple practice. Other measures will be needed for those species that invade without disturbance. For example, Alliaria petiolata is able to germinate, establish and survive in forest interiors (Meekins & McCarthy 2001) and produce seeds under low light (5%) (Meekins & McCarthy 2000). Another invasive, Acer platanoides, has very high seedling establishment (Martin & Marks 2006) and seedling survival (Sanford et al. 2003; Reinhart et al. 2006) in closed canopy sites in deciduous forests. In contrast, invasives that require disturbed conditions for survival as well as establishment should be lower priorities for control, as the invasive should persist only as an ephemeral in newly disturbed sites, although it may suppress the regeneration of natives at such sites.

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