To sprout or not to sprout: Multiple factors determine the vigor of *Kalmia latifolia* (Ericaceae) in southwestern Connecticut

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TO SPROUT OR NOT TO SPROUT: MULTIPLE FACTORS DETERMINE THE VIGOR OF *KALMIA LATIFOLIA* (ERICACEAE) IN SOUTHWESTERN CONNECTICUT

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ABSTRACT. *Kalmia latifolia* has declined in southern New England and other parts of its range in recent decades. This long-term decline is generally attributed to abiotic forces (i.e., low light levels in maturing forests) with little attention to the possible role that top-down effects from ungulate herbivory may be playing. We examined the extent to which mature *K. latifolia* is capable of sprouting under a relatively undisturbed forest canopy—both after severe stem injury and when uninjured—and tested the hypothesis that, in areas with high deer densities, herbivory may exceed abiotic forces in controlling the dynamics of *K. latifolia*. A block design experiment with white-tailed deer (*Odocoileus virginianus*) exclusion and control as treatments and landscape position (hilltop and low slope) as block was established in 2008. Canopy openness was measured in the two treatments within each block using hemispherical canopy photos. Survival and sprouting vigor of cut and uncut *K. latifolia* stems were monitored over 4 years and analyzed using Bayesian Information Criteria model selection with deer herbivory, percent canopy openness, and slope position as predictor variables. Canopy openness and slope position were important drivers of adult *K. latifolia* survival and sprouting capacity, whereas deer herbivory and slope position were the most important drivers of sprouting vigor on cut stems. Our results suggest that in a relatively undisturbed forest with high deer densities, herbivory does not exceed abiotic factors in determining adult *K. latifolia* vigor over the short term, but herbivory and slope position are more important than light in determining sprouting vigor after stem cutting.

Key Words: disturbance, herbivory, *Kalmia latifolia*, light, sprouting, white-tailed deer

Novel disturbance regimes in deciduous tree canopies have resulted in a dramatic increase in evergreen, ericaceous shrubs in the eastern United States during the 20th century. Native and introduced pests and pathogens such as *Cryphonectria parasitica* (Murrill) Barr (chestnut blight), *Lymantria dispar* L. (gypsy moth), and *Dendroctonus frontalis* Zimmerman (southern pine beetle); intensive logging operations; and fire suppression have all contributed to increases in dominant species such as *Rhododendron maximum* L. and *Kalmia latifolia* L. in various parts of their range (Chastain and Townsend 2008; Elliot et al. 1997; League 2005; Monk et al. 1985; Vandermast et al. 2002). *Kalmia latifolia* in particular benefitted from increased light from frequent canopy disturbances over the past century and has become a dominant shrub on dry slopes throughout much of southern New England and the Appalachian Mountain range (Chastain and Townsend 2008; Monk et al. 1985).

In recent decades, however, *Kalmia latifolia* has declined in southern New England and elsewhere in its range (Harrod et al. 2000; Hemond et al.1983). Abiotic factors such as reduced understory light (from reduced frequency and intensity of canopy disturbance) and low soil moisture on dry slopes without recent canopy disturbance have generally been hypothesized to explain declines (Harrod et al. 2000; Hemond et al. 1983; Jaynes 1997; Monk et al. 1985). The extent to which top down effects (higher trophic levels controlling lower levels; Kuijper et al. 2010) by ungulate herbivory have contributed to these declines has generally not been considered.

Kalmia latifolia foliage is toxic to some ungulates and is not a preferred browse species of *Odocoileus virginianus* Zimmerman (white-tailed deer; Conover and Kania 1988; League 2005). However, deer do browse *K. latifolia*, particularly in winter, and can reduce foliage on mature plants and hinder seedling recruitment (League 2005; Levrie et al. 2009).

Basal sprouting is one of the primary modes of reproduction in *Kalmia latifolia* (League 2005). Like many species of the Ericaceae and other woody plants adapted to dry landscapes, *K. latifolia* produces a swollen basal burl or lignotuber at the root crown that is rich in dormant buds, carbohydrates, and nutrients (Del Tredici 2001; Jaynes 1997). Lignotubers facilitate rapid sprouting after stem injury from disturbances such as fire and herbivory (Del Tredici 2001), but some ericaceous shrubs with lignotubers are known to re-sprout continuously in the absence of obvious stem disturbance (Mesleard and Lepart 1989). In addition to uncertainties about the factors that control the development and release of suppressed buds, little is known about what determines how long the buds can remain viable. In some species, the collar retains its sprouting ability into old age, whereas others lose this capacity relatively early in life (Del Tredici 2001). Although old *K. latifolia* are known to sprout when cut back to their base in a cultivated setting (Everett 1981), the shrub's ability to sprout into old age under a shaded forest canopy and while exposed to intensive deer browsing is less clear.

White-tailed deer reach their highest densities in New England in southwestern CT, except for some coastal islands (Adams et al. 2009). Canopy disturbance from logging, insect outbreaks, and other agents are relatively low in this landscape (USDA Forest Service 2013), and thus intensive browsing could hasten the decline of *Kalmia latifolia* here by limiting its ability to sprout vegetatively. Suppression of basal sprouts could be particularly severe because deer tend to browse hardwood sprouts more intensively than seedling plants (Moore and Johnson 1967), and shaded stands of *K. latifolia* are less vigorous and would be expected to sprout less abundantly than those in more exposed locations (cf. Hobbs and Mooney 1985; Del Tredici 2001).

The major objectives in this study were to examine whether aging stands of *Kalmia latifolia* are capable of re-sprouting under a mature and relatively undisturbed forest canopy (i.e., its persistence); and how *K. latifolia* survival and sprouting vigor vary in relation to high deer densities, topographical position, and canopy light. We were particularly interested in testing the hypothesis that top down effects from herbivory may, in some instances, exceed abiotic factors in controlling the vigor of this dominant shrub.

MATERIALS AND METHODS

The study was conducted at Highstead, a 60-hectare woodland preserve in southwestern CT (41.325°N, −73.388°W). The climate consists of cold winters and warm summers with average temperatures of −2.9°C in January and 23.3°C in July and average annual precipitation of 132.4 cm (Northeast Regional Climate Center 2013). White-tailed deer reach their highest densities in the state in southwestern CT and have recently been estimated at ≥23 deer km^{-2} (Kilpatrick 2009). Mature *Quercus* forest (≥100 y old) dominates the western side of the property on rocky slopes of a bedrock ridge. Mature *Kalmia latifolia* dominates the tall shrub layer, which displays a visible browse line. Over the past two decades, *K. latifolia* has declined sharply in this woodland.

We established a block design with deer exclusion and control as treatments and landscape position (hilltop and low slope) as block in Highstead's oak forest. The hilltop block was located on well-drained to somewhat excessively well-drained soils with moderate to very low available water capacity (Natural Resources Conservation Service 2013). Overstory tree species were dominated by *Quercus montana* Willd. with lesser amounts of *Acer rubrum* L. and *Q. rubra* L. The low slope block was located approximately 450 m away from the hilltop block on well-drained soils with moderate to high available water capacity, and was dominated by *Q. rubra* with lesser amounts of *Q. montana*.

To reduce the extent of experimental manipulation (i.e., stem cutting and fencing) throughout Highstead's woodland, we took advantage of two pre-existing deer exclosures, one in each block, in which to conduct the experiment. The hilltop exclosure was 0.18 ha in size and built in 2007, and the low slope exclosure was 0.40 ha in size and built in 1992. The different ages of the exclosures meant that *Kalmia latifolia* stems in the two fenced treatments had been exposed to different durations of browsing prior to the start of the study. The decision to use the exclosures also reduced our overall replication to N = 2 for each treatment and block. However, given the already limited inference of the study (a single property), we decided that concentrating, rather than dispersing, experimental impacts was preferable for this study site. We were also cognizant of the fact that successful experiments at long term research stations have used similar, low-replication designs (cf. Ellison et al. 2010).

In 2008, a patch of mature, live *Kalmia latifolia* was selected at random inside each exclosure and in a control area 50–100 m outside the fence. To test whether aging *K. latifolia* are able to rejuvenate under an intact forest canopy with high deer densities, we cut 21 mature *K. latifolia* stems at approximately 5 cm above ground with a chainsaw in January of 2008. Eleven *K. latifolia* stems were tagged and left intact. Because *K. latifolia* sprouts prolifically from its basal burl when injured (League 2005), we focused our sampling on basal sprouts (hereafter referred to as "sprouts"). In 2008, we counted the number of sprouts (>2.5 cm in length) on cut and uncut stems; on cut stems the sprout clump width and height were also recorded. All measurements were repeated on both cut and uncut stems in 2012. We measured plant heights and basal diameters of tagged *K. latifolia* stems in

Table 1. Initial characteristics of cut and uncut *Kalmia latifolia* stems in each treatment (Treat) and block. Diam. = basal diameter; Hgt. = stem height; HT = hilltop; LS = low slope; FE = fenced; UF = unfenced. No significant differences occurred between treatments or blocks.

	N	Diam. (cm)	SE	ANOVA	Age (yrs.)	SE	ANOVA
Cut stems							
HT	2	5.1	0.1	Treat: F = 0.11;	39.4	2.4	Treat: F = 1.1;
LS	2	5.5	0.1	DF = 1; p = 0.8	40.0	0.1	DF = 1; p = 0.49
FE	2	5.3	0.3	Block: F = 5.4;	38.5	1.5	Block: F = 0.05;
UF	2	5.3	0.1	DF = 1; p = 0.26	40.9	0.9	DF = 1; p = 0.85
Uncut stems					Hgt. (m)		
HT	2	6.5	0	Treat: F = 1;	3.5	0.2	Treat: F = 0.04;
LS	2	5.4	0.15	DF = 1; p = 0.50	3.1	0.1	DF = 1; p = 0.87
FE	2	5.9	0.65	Block: F = 58.8;	3.3	0.3	Block: F = 1.96;
UF	2	6.0	0.5	DF = 1; p = 0.08	3.3	0.1	DF = 1; p = 0.39

each treatment in 2008, and determined the age of each cut stem by counting growth rings. Mean basal diameters, heights, and ages of stems did not differ significantly between treatments and blocks (Table 1). Mean age of cut stems was ~40 y across the study area, indicating the old age of the stand (*Kalmia latifolia's* lifespan is 40–60 y; McNab and Clinton 2013). In August of 2011, three hemispherical canopy photos were taken above both the cut and uncut *K. latifolia* patches in the fenced and unfenced areas of each block. The photos were taken at a height of 1 m above ground in the cut-stem patches and 2 m above ground in the uncut-stem patches. An 8-mm fish-eye lens on a Nikon F-3 film-camera body mounted on a tripod was used (Nikon Corporation, Tokyo, Japan). The photos were analyzed for percent canopy openness using Gap Light Analyzer (Frazer and Canham 1999).

We examined the survival and sprouting vigor of (a) cut and (b) uncut *Kalmia latifolia* stems in relation to three predictor variables: 1) deer (fenced and unfenced); 2) available light (percent canopy openness); and 3) slope position (low slope and hilltop; as a surrogate for soil moisture). Because we were interested in determining the relative support in the data for several competing hypotheses about the effects of herbivory, slope position, and light—rather than identifying significant differences in mean values—we opted to use model selection analysis instead of traditional ANOVA tests (Burnham and Anderson 2004; Hobbs and Hillborn 2006). We also chose Bayesian Information Criterion (BIC) analysis over the more commonly used Akaike Information Criterion (AIC) because BIC provided results for single variable models with a sample size of 2, whereas AICc (the adjusted AIC recommended for small sample sizes; Burnham and Anderson 2004) did not. For each BIC we calculated a Δ_i value using $\Delta_i = BIC_i - BIC_{min}$. This transformation results in $\Delta_i = 0$ for the best model, whereas the other models have positive values. Weights (w_i) were then calculated from $\exp(-0.5*\Delta_i)$ for each model. The sum of w_i was then normalized to equal 1, and each w_i was reported as a probability that a model was the best fit, given the data and the candidate models. Lastly, predictor weights (the sum of all model weights in which a predictor variable occurred) were calculated to determine the relative importance of the predictor variables in explaining each dependent variable (Burnham and Anderson 2004).

For cut stems, we modeled the difference in sprouts per stem, height, and width between 2008 and 2012 (values were calculated from the mean of each of the 21 stems in each year), as well as sprouting success (the proportion of stems with at least one sprout in 2012) in relation to six candidate models (deer, slope position, light, slope position + deer, slope position + light, deer + light). For uncut stems, we modeled adult survival and the difference in basal sprouts per stem between 2008 and 2012 in relation to the same six candidate models. We limited our analysis to single and pairwise combinations because our small sample size (N = 2 treatments and 2 blocks) precluded analysis of the three variables in a full model. We also compared the sprouting height, width, density, and success in 2012 between cut and uncut stems using either paired t-tests for normally distributed data or Wilcoxon signed rank tests for non-normally distributed data. We set alpha equal to 0.05. All data were analyzed using R (version 2.15.2; R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Thirty-seven out of the 44 adult stems (84%) survived in all plots over the course of the 4.5 year study, with 73% survival on the hilltop and 95% on the lower slope. Cut stems generally sprouted more vigorously than uncut stems (Table 2). Eighty of the 84 cut stems (95%) sprouted, versus 41% of uncut stems (Wilcoxon test; $S = -5.0$; $p = 0.13$). Sprout height and sprout width were higher on cut stems than on uncut stems in 2012 by a factor of 4.0 and 10.7 respectively (height: $t = -4.9$; $DF = 3$; $p = 0.016$; width: $t = -5.4$; $DF = 3$; $p = 0.013$; Table 2). There were more sprouts per stem on cut stems than uncut stems by a factor of 5.2 in 2012 ($t = -3.19$; $DF = 3$; $p = 0.049$; Table 2). Sprouting success (the proportion of stems with at least one sprout) did not change over the course of the study for either cut or uncut stems. Mean sprout height and width on cut stems trended upward in all sites over the course of the study, whereas sprout density trended downward. Browsing (percentage of stems with sprouts browsed by deer) was more than twice as common (68%; SE = 26.3) on cut than uncut (30%; SD = 10.0) stems, but the difference was not significant ($t = -2.35$; $DF = 1$; $p = 0.26$). Browsing intensity trended higher on the hilltop than on the low slope for both cut and uncut stems, but statistics were not performed because of lack of replication.

For uncut stems, slope position (greater on low) + light (positive) was the best model predicting adult stem survival, and slope position (greater on low) + light (negative) the best model explaining change in sprouts per stem (Table 3). Bayesian Information Criterion (BIC) weights were low (0.37) for the model predicting adult survival and high (0.97) for the model predicting sprouts per stem. Slope position had the highest predictor weight for adult survival, and slope position and light were similar in their predictor weights for sprouts/stem (Table 4). For cut stems, sprout clump height and width were best explained by deer (negative) + slope position (greater on low slope). The models for sprout height and width had high BIC weights (0.94, 0.98) and therefore, strong probabilities that they were the best model, given the data. Change in sprouts per stem was best explained by deer (negative) + light (positive) with a moderate BIC weight of 0.56; deer had a greater predictor weight (0.94) than did light (0.59; Table 4). Sprouting success was best predicted by slope position (low slope) + light (negative) with a moderate weight of 0.69; slope position had a greater predictor weight (0.96) than did light (0.72; Table 4).

Table 2. Mean values of basal sprouting vigor of cut and uncut stems, and adult survival of *Kalmia latifolia* measured in 2008 and 2012. Sprouts per stem included sprouts ≥ 2.5 cm in length. Sprout success = % of stems with ≥ 1 sprout. Adult survival applies only to uncut stems; sprout height or width applies only to cut stems.

	Treatment/ Block	N	Cut Stems 2008 $\overline{Y}$	Cut Stems 2008 SE	Cut Stems 2012 $\overline{Y}$	Cut Stems 2012 SE	Uncut Stems 2008 $\overline{Y}$	Uncut Stems 2008 SE	Uncut Stems 2012 $\overline{Y}$	Uncut Stems 2012 SE
Sprouts per stem	Hilltop	2	16.9	4.6	7.7	3.1	1.1	0.2	1.6	0.5
	Low Slope	2	25.3	3.8	13.1	2.4	1.3	0.7	2.4	1.8
	Fenced	2	16.9	4.6	10.1	5.5	0.7	0.2	1.3	0.8
	Unfenced	2	25.3	3.8	10.8	0	1.7	0.3	2.7	1.5
	All	4	21.1	3.4	10.4	2.2	1.2	0.3	2.0	0.8
Sprout height (cm)	Hilltop	2	14.0	1.4	29.6	4.2	–	–	8.0	1.9
	Low Slope	2	16.8	0.4	46.7	6.7	–	–	11.1	1.5
	Fenced	2	16.3	1.0	43.6	9.8	–	–	7.8	1.8
	Unfenced	2	14.5	1.9	32.7	7.3	–	–	11.2	1.4
	All	4	15.4	1.0	38.2	5.9	–	–	9.5	1.3
Sprout width (cm)	Hilltop	2	18.3	0.7	54	8.8	–	–	4.8	1.7
	Low Slope	2	29.5	0.3	98.1	16.3	–	–	9.4	3.9
	Fenced	2	23.7	6.1	88.6	25.8	–	–	9.9	3.5
	Unfenced	2	24.1	5.1	63.5	18.3	–	–	4.3	1.2
	All	4	23.9	3.2	76.1	14.8	–	–	7.1	2.2
Adult survival (%)	Hilltop	2	–	–	–	–	100	0	73	9
	Low Slope	2	–	–	–	–	100	0	95.5	4.5
	Fenced	2	–	–	–	–	100	0	82	18
	Unfenced	2	–	–	–	–	100	0	86.5	4.5
	All	4	–	–	–	–	100	0	84.3	7.7
Sprout success (%)	Hilltop	2	90.5	4.5	90.5	4.5	45.5	0	45.5	0
	Low Slope	2	100	0	100	0	36.1	0.1	36.1	0.1
	Fenced	2	93	0.1	93	0.1	36.1	0.1	36.1	0.1
	Unfenced	2	97.5	0.0	97.5	0.0	45.5	0	45.5	0
	All	4	95.3	3.3	95.3	3.3	40.8	4.5	40.8	4.5

DISCUSSION

In a mature *Quercus* forest with high deer densities, an aging population of *Kalmia latifolia* declined in density over 4.5 years, with the rate dependent on available light and slope position. Stems sprouted vigorously when cut at the base. Canopy openness and slope position were relatively important drivers of adult *K. latifolia* survival and sprouting vigor on uncut stems, whereas deer herbivory and slope position were more important drivers of sprouting vigor on cut stems. Our results suggest that in a relatively undisturbed forest

Table 3. BIC analysis used to predict six variables of *Kalmia latifolia* vigor on cut and uncut stems. The lowest BIC value (in bold) corresponds with the best model. Δ_i = the difference in BIC from the best model. w_i = BIC weights - the probability that a model was the best fit, given the data. "Slope" = slope position (hilltop or low slope); "Deer" = fenced or unfenced; Light = % canopy openness. M = model.

	Cut Stems												Uncut Stems					
	ΔSprout Height			ΔSprouts/Stem			Sprouting Success			ΔSprout Width			Adult Survival			ΔSprouts/Stem		
M	BIC	Δ_i	w_i	BIC	Δ_i	w_i	BIC	Δ_i	w_i	BIC	Δ_i	w_i	BIC	Δ_i	w_i	BIC	Δ_i	w_i
Deer	31.4	10.1	0.01	23.6	2.2	0.19	−8.1	8.1	0.01	38.1	11.7	0	−0.7	5.7	0.02	15.0	10.7	0.01
Light	32.6	11.3	0	27.7	6.3	0.02	−9.0	7.2	0.02	39.9	13.5	0	−2.9	3.5	0.06	13.0	8.7	0.01
Slope	28.2	6.9	0.03	27.5	6.1	0.03	−12.1	4.1	0.09	36.1	9.7	0.01	−5.5	0.9	0.24	14.7	10.4	0.01
Deer + Light	32.3	11.0	0	**21.4**	**0**	**0.56**	−8.1	8.1	0.01	39.0	12.6	0	−4.6	1.8	0.15	14.4	10.1	0.01
Slope + Light	29.5	8.2	0.02	28.6	7.2	0.01	**−16.2**	**0**	**0.69**	37.5	11.1	0	**−6.4**	**0**	**0.37**	**4.3**	**0**	**0.97**
Deer + Slope	**21.3**	**0**	**0.94**	23.6	2.2	0.19	−13.5	2.7	0.18	**26.4**	**0**	**0.98**	−4.6	1.8	0.15	15.7	11.4	0.00

Table 4. Predictor weights from BIC analysis of variables used to explain four indices of *Kalmia* vigor in cut stems and two indices in uncut stems. The direction of the relationship is in parentheses, and the best predictor(s) for each index are in bold. Predictor weights are the sum of BIC weights (w_i) of all models in which a predictor variable occurred. See Table 3 for additional information about predictor variables.

	Cut Stems				Uncut Stems	
Variable	ΔSprout Height	ΔSprouts per Stem	Sprouting Success	ΔSprout Clump Width	Adult Stem Survival	ΔSprouts per Stem
Deer	**0.95** (−)	**0.94** (−)	0.20 (+)	**0.98** (−)	0.32 (+)	0.01 (−)
Slope (low slope)	**0.99** (+)	0.23 (+)	**0.96** (+)	**0.99** (+)	**0.76** (+)	**0.98** (+)
Light	0.02 (+)	0.59 (+)	0.72 (−)	0	0.58 (+)	**0.99** (−)

with high deer densities, top down effects do not exceed abiotic factors in determining adult *K. latifolia* vigor over the short term, but herbivory may be more important than light in controlling the shrub's regenerative capacity when cut back to its base.

Not unexpectedly, stem cutting resulted in greater sprouting than on uncut stems in most categories of sprout vigor. That 95% of all cut stems successfully resprouted demonstrates that *Kalmia latifolia* retains an ability to sprout vigorously into advanced age (~40 y, on average in our study area) under a shaded canopy. The same sprouting capacity did not occur with undamaged adult stems, as sprouting success rate remained unchanged and relatively low (41%) over the course of the study. The decline and eventual death of mature *K. latifolia* stems, which occurred predominantly on the hilltop, did not initiate a sprouting response as sometimes occurs in weakened adult *Quercus* spp. and *Populus deltoides* Bart. *ex* Marshall (Oliver and Larson 1996).

Important top down effects on the survival and sprouting dynamics of adult *Kalmia latifolia* were not observed in the 4–5 year time frame of this study. Browsing intensity was low on the sprouts of uncut adult stems (30% of stems), and deer exclusion had little effect on survival rate, change in sprout density, and sprouting success on adult stems. However, deer browsed the sprouts on nearly 70% of cut stems and herbivory was an important factor controlling sprout vigor on cut stems (Table 4). The pattern of herbivory being directed at young, vigorously growing vegetation has been documented for many systems and types of herbivores (Price 1991). However, relatively heavy browsing on young sprouts did not suppress the growth of these sprouts relative to older sprouts on uncut stems (Table 2). Stored resources in the roots of cut stems that are directed to young sprouts apparently both attract and buffer against herbivory, and enable sprouts to outpace less browsed but also less resource-endowed seedlings and sprouts on uncut stems (Del Tredici 2001; Moore and Johnson 1967).

Percent canopy openness was an important negative predictor of sprout abundance on adult stems, whereas light was secondary in importance to slope and deer in predicting adult survival and other variables of sprout vigor. Light as a negative predictor of sprouting abundance is somewhat counter-intuitive, given the well-documented positive response of *Kalmia latifolia* to canopy disturbance and increased light (cf. Chastain and Townsend 2008). However, beneath an undisturbed canopy, adult *K. latifolia* appeared to respond to more stressful, low-light conditions by sprouting more abundantly. *Prunus serotina* Ehrh. (black cherry) has also been reported to sprout abundantly from the base when suppressed under shaded conditions (Auclair and Cottam 1971). That canopy openness varied by only 2.7% above the four patches of uncut stems suggests that *K. latifolia* may be sensitive to relatively subtle differences in canopy light. This response, however, may be typical of vegetation in general, as small variations in light under low irradiance is generally much more important for plants than similar variation under more open conditions (Jennings et al. 1999).

Slope position (low), our surrogate for soil moisture, was the most important overall predictor of *Kalmia latifolia* vigor. Only sprout density on cut stems did not include slope position in the best model or as the strongest predictor (Tables 3, 4). These results accord with Monk et al. (1985), who reported that *K. latifolia* production declined in drier ridge-top locations compared to moister low-slope conditions in the southern Appalachians. That slope position was a better overall predictor of *K. latifolia* vigor than were small variations in canopy openness, also accords with Whittaker (1966) who reported moisture to be a more important driver of plant production than insolation/exposure in undisturbed forest conditions.

It is important to note that the discrepancy in age of the low slope and hilltop deer exclosures reduced our ability to tease apart deer browsing and slope position (i.e., the low slope may have been favorable for *Kalmia latifolia* vigor, in part because of a longer legacy of browsing protection in the fenced treatment). Still, the data suggest that the benefits of longer protection from deer may not have been important with respect to the variables we measured. During the time of our study, cut stems on the low slope had a 100% sprouting rate, regardless of deer protection. In addition, the ratios of both sprout-clump width and height between unfenced and fenced cut stems in 2012 were identical for the hilltop and low slope, suggesting no apparent sprouting advantage for the stems that had longer protection from browsing. Finally, all but one adult stem survived on the low slope over the course of the study.

In its natural state, *Kalmia latifolia* is unlikely to experience severe stem injury under an undisturbed forest canopy, with the possible exception of light surface fires (which are rare in the northeastern forest; Foster et al. 2004) and beaver damage. Our study, therefore, has applications for those who wish to manage aging *K. latifolia* populations in landscapes with high deer densities and relatively infrequent canopy disturbances. Our results underscore the resilience of this shrub when cut back to its base even when top down forces are strong. In the absence of management, declining populations of *K. latifolia* will undoubtedly persist and recover at least some of their vigor over the long term, as forest canopies begin to break up from tree death and disease, and remain more open in advanced stages of development (Oliver and Larson 1996). However, preserve managers may not want to wait that long. Periodically cutting *K. latifolia* back to its base appears to be an effective way to offset the decline of aging stands (cf. Everett 1981), particularly in dry upper slope or hilltop environments, where *K. latifolia* might otherwise die without sprouting at all.

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