



Exploring the Causes of Failed Oak Regeneration in Eastern Deciduous Forests: The Importance
of Historic Disturbance Regimes

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Abstract

Eastern forests are experiencing dramatic shifts in species composition as well as considerable declines in plant biodiversity. Interactions among fire suppression, smaller canopy gaps, and overabundant deer are likely central to these changes. Indeed, only a few years after restoring fire and canopy gaps to the landscape, we often observe increases in plant diversity but only when deer are at moderate densities. The impacts of these altered browsing, fire, and canopy gap regimes and their interactions on forest understory communities in later stages of forest succession are often overlooked. This is a critical oversight because the understory community contains more than 70% of vascular plant diversity. Moreover, we do not understand how fire, gaps, and herbivory interact to mediate forest communities especially as the forest transitions into the stem exclusion stage. This phase is characterized by a dense sapling layer that may be inimical to the herbaceous layer. We tested the hypothesis that the impacts of these processes and their interactions would persist for the woody community but would be transient for the herbaceous community as the forest transitions into the stem exclusion phase. To test this hypothesis, we restored fire, cut canopy gaps, and excluded deer using a split-plot, fully factorial experiment. We then measured the response of >21,000 stems representing >150 species after twelve years.

For saplings, we found that browsing caused a decline in species richness and diversity. Specifically, when we excluded deer, sapling diversity doubled under open canopies. For herbaceous species following fire, browsing increased species richness by approximately 40% likely mediated by reducing a dominant, fast-growing shrub (*Rubus allegheniensis*). We are the first to demonstrate that long-term interactions among disturbances and herbivory simultaneously cause contrasting responses in the herbaceous versus the sapling layer. We suggest that diverging understory responses to disturbances are driven by high stem

density of the sapling layer that drives down both above- and belowground resource availability in the herbaceous layer.

Key words – disturbance, fire, canopy gaps, browsing, stem exclusion phase, diversity, bottleneck

Background/Question/Methods

Conventional models of early forest development describe a simplified transition from an initially resource rich environment to one of intense sapling competition that creates a bottleneck for understory plant abundance and diversity. These models of succession are commonly accepted as dogma but poorly understood and seldom tested. The initial years following disturbance (i.e., stand initiation stage) are often characterized a dense and species rich herbaceous layer. The changes in the herbaceous layer are driven by increases in resource (e.g., light) and microsite availability as well as the stimulation of germination from the seed bank. After 8 to 15 years, however, as the forest stand enters the stem exclusion phase, the dense regenerating sapling layer is predicted to greatly restrict understory resources and cause herbaceous cover, richness, and diversity to plummet, often to pre-disturbance levels. When this occurs, species that initially colonized after the disturbance are displaced by the dense sapling layer and may be locally extirpated if there is a lack of propagules in the seed bank or at adjacent sites. Thus, the stem exclusion phase may represent an important bottleneck for the maintenance of herbaceous layer diversity, though this has rarely been explicitly tested, particularly in eastern forests.

Here, we present the results of a comprehensive, long-term investigation testing how interactions among fire, canopy gaps, and deer herbivory affect abundance and diversity of both saplings and the herbaceous layer. Our prior work in the early years post-disturbance demonstrates unequivocally that understory fires and canopy gaps, alone and in concert, increased tree and herbaceous layer richness and abundance and altered composition^{1,2}. Moreover, we found deer browsing nullified the benefits of disturbance on tree diversity but enhanced the benefits of disturbance on herbaceous diversity. Here, we build on these earlier results by examining if the legacy of the factors that shaped plant communities during early establishment and subsequent growth is evident in stands as they enter the stem exclusion stage.

In size-structured communities such as trees, successional theory predicts that initially abundant species will remain dominant through the stem exclusion stage and species compositional changes will accrue slowly as more shade-tolerant species enter the canopy. Hence, predict the effects of disturbance and browsing observed during the stand initiation phase will persist in the sapling layer during the stem-exclusion stage. In contrast, if high sapling densities and canopy closure greatly restrict understory resources, we predict the initially strong signal of disturbance and herbivory on herbaceous species richness, abundance, and composition will wane and potentially vanish.

Study Description and Location

Site characteristics - We tested these hypotheses near the geographic center of the eastern deciduous forest using a fully factorial experiment implemented for 12 years at locations in Tucker County, northeastern West Virginia. There are a total of four stands; two on the Monongahela National Forest (39°80'60" N, 79°84'30" W) and two others at the Fernow Experimental Forest (39°80'10" N, 79°84'20" W). Stands range in size from 10 to 40 ha and from 670–810 m elevation. Stands were second-growth forests (60–90 years old) and predominantly upland sites including ridge tops and slopes (0–31%; 14.1% ± 0.9% [mean ± SE]). Stands are dominated by *Quercus rubra* L., *Q. alba* L., and *Q. montana* L. and include *Acer saccharum* Marsh., *A. rubrum* L., *Prunus serotina* Ehrh., *Fagus grandifolia* Ehrh., *Tilia americana* L., and *Betula lenta* L. as associated canopy species. The herbaceous layer is species rich (144 species). The deer population ranges from 4.6 to 7.7 deer/km² (M. Ford, personal communication).

Experimental treatments - Canopy Gaps, Deer Exclusion, and Prescribed Burns

In 2000, we simulated canopy gaps consistent in size to what is common in old-growth stands (ca. 280 m²). We created the gaps by girdling trees >10 cm diameter at breast height

(DBH) inside the center 18 m x 18 m of 32 plots and injecting them with herbicide (Accord by Monsanto, St. Louis, Missouri, USA). All girdled trees were either dead or almost entirely defoliated within twelve months of treatment. We surrounded 32 of the 20-m x 20-m plots with wire mesh fences (2 m high, mesh size: 15 cm x 15 cm or 15 cm x 30 cm) in 2000. These fences proved highly effective at excluding deer. In late April and early May 2001, we burned a randomly chosen side of each of the four stands (5-20 ha/side). We chose this time period because it was during peak fire season, which is during sapling bud break but just prior to the canopy bud break. These were similar in temperature and severity to a typical surface fire.

Data Collection

We censused the woody stems in each plot in the summer of 2013. We identified and recorded all stems ≥ 140 cm tall and with a diameter at breast height (DBH; measured at 140 cm) and ≤ 5 cm DBH throughout the entire 20-m x 20-m plot; these established saplings are most likely to make up the future canopy. In July 2013, we censused the density and estimated percent cover of herbaceous vegetation within five randomly located permanent 1-m x 1-m quadrats within the inner 10-m x 10-m area of each plot. We performed a meander survey of the central 10-m x 10-m area of each plot to determine the herbaceous species richness. To incorporate rarer species into our calculations of diversity, we averaged percent cover data across all subplots within each plot and incorporated the species not found within the subplots but via the meander survey as 0.01% cover. Only vascular plants with life history characteristics that confine them to the ground layer (< 1.5 m tall) were included in this part of the survey. This included shrubs, ferns, forbs, and graminoids.

Finally, to estimate the degree of canopy closure, we obtained leaf area index (LAI) measures in plot using a quantum point sensor (LAI 2000 LiCorr, Inc., Lincoln, NE) between June and August 2001 and again in July 2014. We took evenly spaced readings within each 20-m x 20-m plot 1 m above the forest floor and used a second sensor to take above canopy readings

simultaneously in a nearby clearing. We performed 8 readings per plot in 2001 and 12 readings per plot in 2014.

Data Analysis

We used split-plot ANOVAs within randomized blocks using PROC GLIMMIX in SAS 9.3 to determine the effects of all treatments and interactions on the sapling and ground layer vegetation abundance, richness, and diversity as well as seed bank abundance and richness. We determined the density of saplings and the percent cover of the herbaceous layer and calculated species richness and Shannon diversity (e^H). As some of our predictions test changes in abundance, richness and diversity that occur as areas transition into the stem exclusion stage, we utilized data from prior censuses to calculate rates of change. We calculated the absolute change in saplings/ha between 2002 and 2013 ($N_{2013} - N_{2002}$; Collins and Carson unpublished data) as well as the change in percent herbaceous cover, richness, and diversity between 2006 and 2013 ($x_{2013} - x_{2006}$; Royo et al. 2010).

We modeled the main treatments, browsing, fire, and canopy gap, as fixed effects and stand and fire \times stand interactions as random effects. We used negative binomial distributions for all models of stem density, beta distributions for all models of herbaceous cover, and Gaussian distributions for all other models. In addition, we used Gaussian distributions for all models testing the absolute change in sapling and herb layer abundance over time. We simplified the models by removing non-significant interactions ($P > 0.05$) from the analyses one by one, beginning with three-way interactions and removing two-way interactions from the highest to lowest P-value. All main effects (fire, gap, browsing) were kept in the model regardless of significance level.

To determine differences in species composition among treatments, we performed Permutational Multivariate Analysis of Variance (perMANOVA) via ADONIS using the *vegan*

2.0 package in R 3.0.2. We then identified the species most responsible for any differences among treatments via similarity percentage analysis (SIMPER) of the absolute abundance of each contributing species. We stratified the model with fire×stand and ran 3,000 permutations then simplified the model by removing non-significant interactions as stated above. Because of the limitations of this multivariate technique, plots with 0 stems or 0% herbaceous cover were removed from the analyses; therefore, the design was unbalanced. The statistical analyses were developed in collaboration with and reviewed by John Stanovick, the FS Northern Research Station statistician and were utilized in two publications from this project (Royo et al. 2010, Nuttle et al. 2013).

Key Findings

Across all plots, we sampled ca. 16,000 woody and ca. 5,000 herbaceous plants representing 46 and 114 species respectively: 21 canopy species and 25 sub-canopy tree species (e.g., tree species that rarely reach the canopy), 10 fern species, 70 forb species, 9 graminoid species, and 25 shrub species. Trace amounts of two invasive species (*Rosa multiflora*, *Berberis thunbergii*) were documented across the entire experiment. Over the course of the experiment, light levels decreased in gaps. In 2001 canopy gaps decreased the leaf area index 1 m above forest floor by 26%. By 2014, LAI was equivalent across all treatment combinations, likely indicating canopy closure in gap plots over the course of the experiment.

Sapling Community

In browsed areas, canopy gaps created a dense and species rich, but low diversity, sapling layer composed primarily of *Betula lenta* and *Acer pensylvanicum*. Between 2002 and 2013, canopy gaps increased sapling density two-fold regardless of deer browsing (ca. 300 stems/plot) relative to under a closed canopy. Moreover, under a closed canopy, browsing reduced sapling density by ca. 50%. Although canopy gaps increased sapling richness ca. 4 species/plot ($P < 0.0001$ and the relative abundance of shade-intolerant species (no gap $16.33\% \pm 6.75\%$, vs. gap

25.41% \pm 6.75%; $P = 0.0464$), but sapling diversity increased only in the absence of deer ($P = 0.0482$). Browsing caused the formation of a sapling layer that was dominated (ca. 80%) by *B. lenta* and *A. pensylvanicum*. In contrast, excluding browsers reduced the relative abundance of these two species to ca. 35%. In addition, canopy gaps and browsing together caused a significant, yet minor shift in species composition (perMANOVA: $R^2 = 0.025$, $P = 0.0318$).

Understory fires increased sapling density between 2002 and 2013 five-fold. Fire doubled the richness and diversity of large saplings (Richness: $P = 0.0229$, Diversity: $P = 0.0037$) and doubled relative abundance of shade-intolerant sapling species ($P = 0.0217$), but only in the absence of browsing. In addition, fire reduced the relative abundance of *A. pensylvanicum* by 75% ($P=0.0188$) and of all shade-tolerant species combined by 50% ($P = 0.0115$) in the absence of deer. Canopy gaps and fire together increased sapling density 4 \times when compared to control plots ($P = 0.0039$) and caused a minor shift in species composition (perMANOVA: $R^2 = 0.025$, $P = 0.0287$).

Browsing alone decreased sapling species richness by ca. 33% ($P = 0.0003$), and quadrupled the relative abundance of *Betula lenta* ($P = 0.0258$). SIMPER analysis revealed that fire shifted sapling composition by increasing the absolute abundance of *Liriodendron tulipifera* and *Aralia spinosa* 28 \times and 26 \times respectively, while doubling *Acer pensylvanicum* and *Betula lenta* (perMANOVA: $R^2 = 0.14$, $P = 0.0001$). Gaps increased the absolute abundance of *A. pensylvanicum* 2 \times and *B. lenta* 4 \times , but had little effect on the absolute abundance of most other species (perMANOVA: $R^2 = 0.062$, $P = 0.0001$). Browsing decreased *L. tulipifera* by 66%, *Acer rubrum* by 50%, and *A. spinosa* by 75%, but increased *B. lenta* 300% (perMANOVA: $R^2 = 0.027$, $P = 0.0215$).

Herbaceous Community

Between 2006 and 2013, herbaceous cover under canopy gaps or in burned areas decreased by 15% decline in herbaceous cover. Where fire and gaps co-occurred, herbaceous

cover declined by ca. 35% over the 7-year period and the drop was particularly strong in browsed areas (a significant three-way interaction). The increase in sapling density between 2002 and 2013 explained 30% of the variation in the decline in herbaceous cover, strongly suggesting that as the regenerating tree community was entering into the stem exclusion stage it was causing a concomitant collapse in the herbaceous community ($R^2 = 0.3007$, $P < 0.0001$).

Following fire, browsing increased herb richness and diversity, but decreased the relative abundance of *Rubus*. Browsing and fire together increased herb species richness by 40% and increased herb diversity by 30% (Richness: $P = 0.022$, Diversity: $P = 0.0118$). In particular, browsing and fire together doubled the richness and diversity of ferns (Richness: $P = 0.0087$, Diversity: $P = 0.0406$). When we excluded browsers, fire increased the relative abundance of *Rubus* from 15% to 48% ($P = 0.0009$). No single process—fire, canopy gaps, or browsing—had any effect on the overall richness, diversity, cover, or composition of herbaceous species in 2013.

Relationship to other recent findings

Our study is the first experimental test of long standing conventional models of forest succession. We demonstrate that the rapid increases in sapling density following disturbance led to precipitous declines in herbaceous cover. The declines were so pronounced that by 2014, we detected no effects of disturbance of browsing on herbaceous richness or diversity. In addition, we found that browsing exacerbated the decline in herbaceous cover following co-occurring disturbances. Traditional models of early forest development describe a simplified transition from a resource rich environment following disturbance to one of intense sapling competition creating a bottleneck for understory plant biomass and diversity³⁻⁹. These conventional models are largely untested, and more recent criticisms have suggested they overlook the implications of incomplete closure of the sapling canopy, particularly following less severe or patchy disturbances (e.g., surface fires and small canopy gaps^{6,9,10}). Moreover, these models entirely

overlook the evidence that browsing can shift successional trajectories to form communities composed of browse-tolerant and unpalatable species¹¹⁻¹³. The lack of a uniformly closed sapling canopy during the stem exclusion phase likely allows for the persistence of a host of herbaceous species that established immediately following disturbance, even as herbivores reduce herbaceous cover and sapling diversity.

Management Implications

If forest managers are interested in reversing the downward trend in diversity of regenerating mixed mesophytic forest our results show the reintroduction of fire and canopy gaps, often in combination, are critical. The reintroduction of these disturbances enhanced the abundance and diversity of both the tree community and the herbaceous community. However, our results also demonstrated that managing deer browse pressure is also clearly in order. Browsing negated the benefits of gaps on sapling density and diversity, enhanced herbaceous layer diversity following fire, and ultimately limited herbaceous cover as stands entered the stem exclusion phase. These results suggest managers may tailor their treatments or combinations of treatments to meet specific management objectives. For example, if abundant and diverse tree regeneration is desired, achieving these goals will require large canopy openings in combination with reduction of browsing by deer in areas of high deer density. However, if the maintenance of overall plant biodiversity is a preeminent objective, understories burns with or without canopy openings combined with moderate browse pressure may be more appropriate. Deer browsing can be reduced by fencing to exclude browsing following timber harvest or by reducing regional deer density through effective population management. Given that our results document the total exclusion of deer may limit herbaceous diversity, we suggest that a regional reduction in deer densities is a reasonable management goal if maintenance of forest diversity is a priority.

Future work needed

Over the course of 12 years of forest succession, the effects of co-occurring disturbances

continue to enhance sapling layer richness and diversity, but caused only an ephemeral pulse in herbaceous layer abundance. Moreover, browsing often mediated the degree and rate of these changes: weakening them in some cases, enhancing them in others. Historically, all of these processes (large canopy gaps, understory fire, and browsing) almost certainly occurred in a mosaic across the landscape. We suggest that this heterogeneity would have contributed substantially to an array of habitats and conditions and thus helped promote diversity in understory communities that represent >75% of the vascular species richness in many temperate forests. Future work is needed to determine if, in fact, the variation in disturbances and browse pressure at larger scales promotes diversity. Moreover, it is also not clear whether the ephemeral increases in herbaceous diversity and abundance following disturbance would buffer populations of these species through the establishment of individuals in adjacent areas or via a replenishment of propagules in the seed bank.

In order to address these outstanding questions, we are currently working on two related projects. First, in 2013, we sampled the seed bank in all experimental plots. These seed bank samples were brought to the USDA Forestry Sciences Laboratory in Irvine, PA and we conducted emergence trials for 18 months to quantify seed bank richness and abundance. Results from this work are currently being analyzed and will shed light on the outstanding question of whether the pulse in herbaceous recruitment following disturbances was sufficient to provide a buffering mechanism to the collapse in herbaceous abundance that occurred following entry into the stem exclusion stage. Additionally, In June 2015, we established a new set of 4 large-scale control stands distinct from the original stands containing the experiment. These sites were paired to the existing 4 experimental stands based on similar area (10-40 ha), slope, aspect and elevation. Within both the experimental stands and the newly established control stands we conducted a full species inventory (woody and herbaceous) within 4 randomly chosen 100 m² subplots in each of the stands (Total of 32 subplots: 4 control stands × 4 subplots + 4

experimental stands × 4 subplots). Data from these surveys will help us address whether the heterogeneous disturbance and browsing conditions created within the experimental landscape enhanced biodiversity relative to undisturbed and browsed areas in otherwise identical landscapes.

Finally, our experimental design utilized only one fire at the onset of the experiment. Since historically, fire return intervals on oak dominated sites are on the order of a few years to a few decades, we are actively engaged in planning a second fire within the experiment to test how recurring fires alter successional dynamics and patterns of biodiversity.

Deliverables Crosswalk Table

Deliverable Type (see proposal instructions)	Description	Delivery Dates
Active: Training Sessions	Since 1978 scientists from NRS-02 have conducted weeklong training sessions annually that have included > 1600 representatives from industry and state and federal agencies that show managers how to integrate research results into improved, sustainable management practices (SILVAH & OAK SILVAH). These sessions are a model for similar programs in the eastern US, including West Virginia, Ohio, and Kentucky. Results from the proposed work will be incorporated into these sessions.	Results from this work have not yet been incorporated into the SILVAH training sessions. However, we note that last year's Allegheny SILVAH session was cancelled, so the opportunity to incorporate these results were curtailed. We plan on moving forward with incorporating results as data develops and sessions recommence.
Active: Professional Meetings	All PI's are committed to and will share responsibility in disseminating information from this project at local, regional, and	Work from the project has been disseminated through offered and invited talks at universities and international meetings. A list of talks follows: 1. Royo, A.A. 2013. Challenges of sustainable forest management amidst the interacting forces of northern temperate forests. 2013 Ecological Society of America Annual Meeting, Minneapolis,

	national/international meetings.	<p>MN. (<i>Talk was part of a special session</i>). August 4-9, 2013.</p> <ol style="list-style-type: none"> 2. Royo, A.A. 2014. Picking the higher hanging fruit: Deer-vegetation research innovations. Northern Research Station Communications and Science Delivery Team. January 7, 2014. 3. Royo, A.A. 2014. Fire, Gaps, and Deer: The roles of multiple interacting disturbances in eastern hardwood forests. Univ. of Vermont-Rubenstein School of the Environment and Natural Resources. April 17, 2014. 4. Royo, A.A. 2014. Interactions among deer and disturbances control plant dynamics in mixed mesophytic forests. State University of New York-ESF, Adaptive Peaks Seminar. April 24, 2014. 5. Royo, A.A. 2014. The roles of multiple interacting disturbances in eastern hardwood forests. University of Missouri-Columbia, School of Natural Resources. May 2, 2014. 6. Royo, A.A. 2014. L'union fait la force: Disturbance and herbivory interactions govern plant species diversity in mixed mesophytic forests. Université Laval, Quebec, Canada. May 30, 2014. 7. Royo, A.A. 2014. The Forest Above and Below: Disturbance and herbivory interactions govern vegetation and seed bank diversity. Ohio State University, Department of Biology. November 6, 2014. 8. Royo, A.A. 2015. The Forest Above and Below: Disturbance and herbivory interactions govern vegetation and seed bank diversity. Penn State University, Department of Biology. January 23, 2015. 9. Carson, W.P., Nuttle, T., Royo, A.A., Adams, M.B., Chips, M.J., and Wenzel, J. 2015. On the causes and consequences of changes in the browsing and disturbance regimes across the Eastern deciduous forest biome. Symposium: The Ecological and Silvicultural Consequences of Disturbance and Salvaging on the Sustainability and Biodiversity of Forest Ecosystems. Powdermill Nature Reserve; Rector, PA. May 29 – 31, 2015. (<i>Talk was part of an symposium co-organized by Royo</i>) 10. Carson, W.P., T. Nuttle, A.A. Royo, and M.B. Adams. On the causes and consequences of changes in the dynamics and disturbance regimes across the eastern deciduous forest. 2015 Ecological Society of America Annual Meeting. Baltimore, MD. (<i>Talk was part of an organized oral session</i>). August 9 – 14, 2015. 11. Royo, A.A. 2014. Deer browsing negates storage effect following disturbance. Society of American Foresters Annual Meeting. Salt Lake City, UT. October 12, 2014. 12. Barry, K.E. Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests. 4/24/15. University of Wisconsin-Milwaukee - Department of Biological Sciences Colloquium. Milwaukee, WI. 13. Chips, M.J. A.A. Royo, T.J. Nuttle, M.B. Adams, and W.P. Carson. 2015. The stem exclusion bottleneck: identifying the key drivers of plant diversity in temperate forests. Ecological Society of America Annual Meeting. Baltimore, MD. August 9 - 14, 2015. 14. Barry, K.E. & Schnitzer, S.A. Are we missing the forest for the trees? Spatial patterns of diversity in temperate deciduous forests. 11/10/15. University of Pittsburgh. Advanced Ecology Seminar Series. 15. M. J. Chips, A. A. Royo, T. Nuttle, M. B. Adams, and W. P. Carson. March 2014. A tale of two communities: Moderate browsing reduces tree diversity but enhances herbaceous diversity under historic disturbance regimes. The University of Pittsburgh. 16. M. J. Chips, A. A. Royo, T. Nuttle, M. B. Adams, and W. P. Carson. October 2014. A tale of two communities: Moderate browsing reduces sapling diversity but enhances herbaceous diversity. The Wildlife Society (Presentation).
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Active: Field tours	This experiment's research plots are frequently used as tour stops to university and professional visitors to the Fernow Experimental Forest (see Support Letters).	Ongoing
Passive: Publications	We expect at least two high-quality peer-reviewed scientific papers from this project: an herb dynamics paper (Royo, lead) and a tree dynamics paper (Nuttle and Thomas-VanGundy leads).	<p>Since funding, we have completed one publication using previously collected data from the project:</p> <p>Nuttle, T., Royo, A.A., Adams, M.B., and W.P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forests. <i>Ecological Monographs</i>. 83(1): 3 – 17.</p> <p>A second publication (Chips et al., in prep) is expected. This will contained within a Special Issue devoted to Long-term studies in the central hardwood region following presentation of the results at the Central Hardwoods Conference in March 2016.</p> <p>Other publications on the influence of treatments on seed bank dynamics and the disturbance matrix will be forthcoming. In addition, there will be a separate manuscript on the effect of disturbance and herbivory treatments on shaping negative density dependence mechanisms (K. Barry, Ph.D. student, Univ. of Wisconsin – Madison)</p>

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