2016

Herbivory and Advance Reproduction Influence Quaking Aspen Regeneration Response to Management in Southern Utah, USA

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NRC Research Press

ARTICLE

Herbivory and advance reproduction influence quaking aspen regeneration response to management in southern Utah, USA

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Abstract: Recent concern regarding the potential decline of quaking aspen (*Populus tremuloides* Michx.) forests in the western United States has sparked concern over whether the species can be effectively regenerated. Using a retrospective approach, we quantified the response of regenerating aspen stems to an ordinary set of silvicultural treatments conducted over approximately the past decade in southern Utah, USA. A suite of variables describing stand structure and composition, stand vigor, physiographic factors, herbivore pressure, and treatment types were measured to predict the possible controls, as well as their relative importance, on aspen regeneration. Results suggested that aspen regeneration was most strongly related to browsing pressure, site preparation technique, and the presence of advance reproduction before treatment, which is a novel finding. Secondary predictors included elevation, site index, and overstory conditions, which are generally characteristics of stand vigor. Management recommendations based on our results should recognize the strong primary control that browsing pressure exerts on regeneration. First, the height of advance reproduction is inherently dependent on antecedent herbivory and also indicative of present browsing and should be assessed before treatment. Second, the most effective site preparation techniques, namely broadcast burning and browsing reduction, will directly reduce browsing pressure, assuming ungulate populations are not too large. Any management targeting timely and effective aspen regeneration should incorporate monitoring and (or) controlling browsing pressure, both before and after treatment.

Key words: browsing, coppice, herbivory, *Populus tremuloides*, silviculture.

Résumé : L'inquiétude récente face au dépérissement appréhendé des forêts de peuplier faux-tremble (*Populus tremuloides* Michx.) dans l'ouest des États-Unis a suscité un questionnement concernant la possibilité de régénérer efficacement cette espèce. À l'aide d'une approche rétrospective, nous avons quantifié la réponse de tiges de peuplier faux-tremble au stade de la régénération à un ensemble ordinaire de traitements sylvicoles réalisés au cours de la dernière décennie dans le sud de l'Utah, aux États-Unis. Une série de variables décrivant la composition et la structure du peuplement, la vigueur du peuplement, les facteurs physiographiques, la pression des herbivores et les types de traitement ont été mesurées dans le but de déterminer quels facteurs pourraient influencer la régénération du peuplier faux-tremble ainsi que leur importance relative. Les résultats indiquent que la régénération du peuplier faux-tremble est surtout influencée par la pression des herbivores, la préparation technique du terrain, et la présence de régénération préétablie, c'est-à-dire avant le traitement, ce qui constitue un résultat inédit. Les prédicteurs secondaires incluent l'altitude, l'indice de qualité de station et l'état de l'étage dominant: généralement les caractéristiques de vigueur du peuplement. Selon nos résultats, les recommandations d'aménagement devraient reconnaître que la régénération est contrôlée principalement par la pression des herbivores. Premièrement, la hauteur de la régénération préétablie dépend intrinsèquement du broutage passé mais peut aussi donner une idée de l'impact actuel du broutage; elle devrait être évaluée avant d'appliquer un traitement. Deuxièmement, les techniques de préparation de terrain les plus efficaces: le brûlage extensif et la réduction du broutage, réduiront directement la pression des herbivores à condition que les populations d'ongulés ne soient pas trop importantes. Tout aménagement visant à établir une régénération en temps opportun et efficace du peuplier faux-tremble devrait comprendre le suivi ou le contrôle de la pression des herbivores, ou les deux, avant et après le traitement. [Traduit par la Rédaction]

Mots-clés : broutage, taillis, herbivorisme, *Populus tremuloides*, sylviculture.

Introduction

Quaking aspen (*Populus tremuloides* Michx.; hereafter, aspen) is an ecologically and economically important forest species throughout its range (Baker 1925). A prevalent theme in the aspen literature is concern for the timely regeneration and recruitment of aspen (Long and Mock 2012), and this is perhaps more relevant as environmental perturbations associated with "sudden aspen decline" (Worrall et al. 2013) and warming temperatures (Rehfeldt et al. 2009) increasingly threaten aspen forests. A multitude of factors potentially influence the quality and quantity of regenerating aspen in natural and managed systems. Demographic processes such as timing of stand establishment and succession to conifers and associated mortality can profoundly influence the ability of aspen to regenerate (Smith and Smith 2005; Kaye 2011; Calder and St. Clair 2012). A lack of fire in what are thought to be primarily fire-driven ecosystems (Shinneman et al. 2013) can also influence the perception of limited young aspen forests. Excessive and (or) long-term browsing by herbivores has been widely documented as negatively affecting both the quantity and quality of

Received 5 January 2016. Accepted 5 March 2016.

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aspen suckers (Kay and Bartos 2000; Seager et al. 2013; Rogers and Mittanck 2014). However, the recognition that multiple interacting disturbances such as fire and herbivory can have both positive and negative effects on aspen communities further complicates the issue (Kaye et al. 2005; Kulakowski et al. 2013; Wan et al. 2014*b*, 2014*a*). Despite this large body of work, studies that integrate multiple possible controls on aspen regeneration into our understanding of aspen regeneration ecology can provide unique insight and help guide contemporary management recommendations.

Aspen exhibits vegetative suckering, a unique and effective adaptation to disturbance-prone environments based on the disruption of growth hormones in the plant (Wan et al. 2006), that can result in a prolific response (thousands of shoots per hectare) to overstory removal. As such, traditional aspen regeneration treatments (i.e., coppice) tend to mimic ecological processes known to promote aspen suckering observed under natural circumstances (Baker 1918; O'Brien et al. 2010; Long and Mock 2012). In this sense, coppice systems are an analog to stand-clearing disturbances, e.g., fire, which is likely the primary disturbance regenerating aspen (Shinneman et al. 2013). Heterogeneity in wildfire characteristics results in highly variable aspen regeneration, including sexual versus asexual reproduction (Romme et al. 2005) and densities that differ by orders of magnitude (Smith et al. 2011; Wan et al. 2014*b*) in response to fire severity (Keyser et al. 2005). Although other noncoppice options exist for regenerating aspen (e.g., prescribed fire, mechanical root stimulation, and removal of competing vegetation (Sheppard 2001, p. 200)), like wildfire, they are likely to result in substantial variability in densities.

In addition to stand-replacing disturbances, there are other important factors that play a role in the quantity and quality of regenerated aspen stems. For example, the overall condition or vigor of aspen stands is thought to influence regeneration potential (Sheppard 2001). Although vigor cannot be measured directly, there are quantifiable surrogates. For example, previous assessments of aspen have used canopy cover as a proxy for stand vigor (Worrall et al. 2008, 2010). At the tree and stand levels, more precise assessments of vigor might include radial growth, site index as an indicator of potential productivity, sapwood area as a surrogate for leaf area, the abundance of advance reproduction, or the proportion of conifers in the overstory and (or) understory (Rogers et al. 2014). With respect to regenerating aspen, stand vigor might also dictate the rate at which suckers would attain heights that reduce their susceptibility to ungulate browsing pressure.

Herbivory by ungulates has long been known to be one of the most important factors influencing regeneration and recruitment in western aspen stands (Bartos and Campbell 1998; Seager et al. 2013). Excessive herbivory from both native and domestic ungulates can cause dramatic reductions in young aspen stems. Native ungulate species known to browse aspen include deer (*Odocoileus hemionus* (Rafinesque, 1817)) and elk (*Cervus elaphus* Linnaeus, 1758), whereas sheep (*Ovis aries* Linnaeus, 1758) and cattle (*Bos* spp.) are common domestic ungulates. Various combinations of these ungulate species, at high densities and during specific seasons, can have significant impact on understory or regenerating aspen (DeRose and Long 2010). Indeed, recent work in eastern Utah indicated that problems with successful aspen recruitment were due, at least in part, to herbivory (Rogers and Mittanck 2014). Fortunately, herbivores tend to have much less impact on aspen stems as they grow taller, which is why height thresholds are often invoked to identify regeneration that is likely to contribute to the future overstory (Bartos et al. 1983).

In this study, we retrospectively quantify pre- and post-harvest stand conditions within relatively recent (up to a decade old) silvicultural treatments that had the explicit goal to regenerate aspen in southern Utah, USA. We simultaneously explore a suite of tree, stand, and physiographic factors that are likely to affect aspen regeneration to address three hypotheses: (*i*) that the silvicultural regeneration method will have an effect on regeneration, (*ii*) that stand vigor will have a positive effect on regeneration, and (*iii*) that herbivore pressure will have a detrimental effect on regeneration. Through the identification of the primary drivers on regenerating aspen and their relative importance, we can suggest practical recommendations to improve the effect of common regeneration methods on aspen regeneration.

Methods

Study area and site selection

The study area included Cedar Mountain and the Cedar City Ranger District (CCRD) on the Dixie National Forest. Cedar Mountain is largely privately owned and encompasses approximately 275 km^2 of the Kolob Terrace formation. The CCRD occupies approximately 1400 km^2 of the Markagunt Plateau, and both jurisdictions fall within the Colorado Plateau region in southwestern Utah. Snowfall, delivered primarily by Pacific-origin westerlies, brings most of the precipitation during the winter months. The study area also receives monsoonal rainfall during the summer months. Major forest types consist of a mosaic of aspen and aspen–conifer mixtures. Conifer associates included Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hilebr.), blue spruce (*Picea pungens* Engelm.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.).

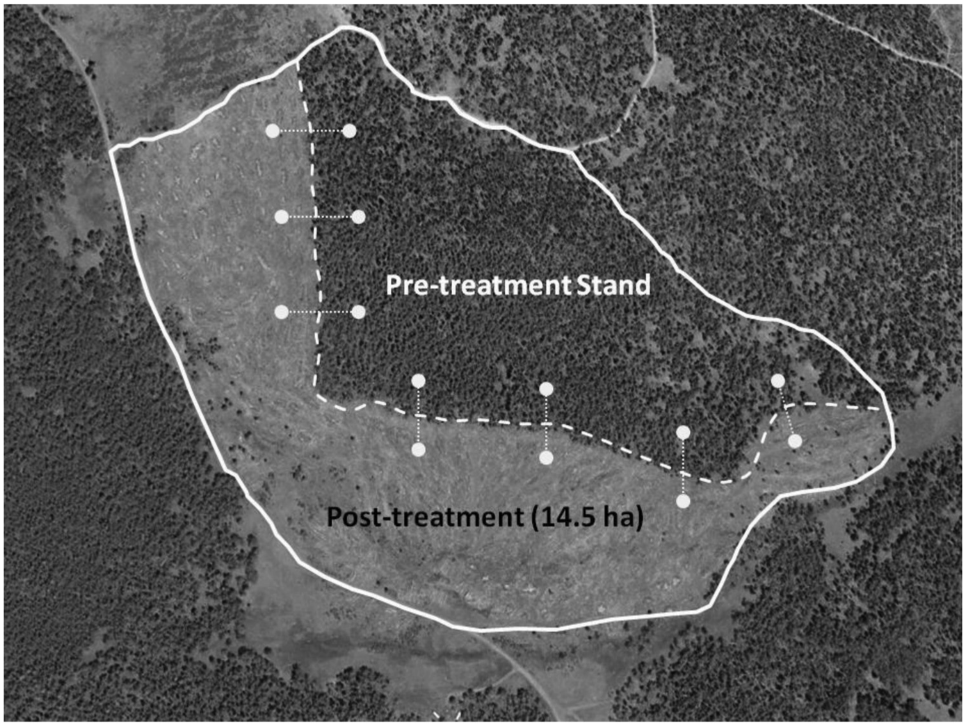
The selection of research sites was facilitated through a collaborative effort with the U.S. Forest Service, the Utah Department of Forestry, Fire, and State Lands, and private landowners. The collaboration included land managers involved in the implementation of aspen regeneration treatments on Cedar Mountain and the CCRD. Sheep grazing has a long history on Cedar Mountain, stemming from multigenerational family tradition (Bowns and Bagley 1986), and these landowners have typically regenerated aspen for aesthetic purposes. Aspen management on the CCRD was motivated primarily by the need to respond to Engelmann spruce mortality caused by the previous two decades of the spruce beetle (*Dendroctonus rufipennis* (Kirby, 1837)) epidemic (DeRose and Long 2007).

Because we sought to quantify the response of aspen regeneration to a range of silvicultural treatments, sample sites were limited to stands where the goal of the treatment was to regenerate aspen and a reasonable portion (at least 25%) of the pre-harvest stand was left intact (determined from aerial imagery and field reconnaissance). All regeneration treatments occurred during the growing seasons of the years 2001 through 2012; therefore, our sampling was retrospective. Regeneration treatments included prescribed fire ($n = 4$), conifer removal ($n = 4$), removal of declining or dead overstory aspen ($n = 9$), and complete overstory removal or coppice ($n = 83$). Because historical documentation was not always clear, we determined that, in nearly all regeneration treatments, overstory trees were felled with a feller buncher and sometimes by hand felling; however, in all cases, stems were yarded with rubber-tired skidders. Many of the treated areas received subsequent site preparation, i.e., post-harvest manipulation to enhance the success of regeneration (Helms 1998). As determined from historical documents, three site preparation techniques were implemented: broadcast burn ($n = 25$); pile and burn ($n = 22$); and relief from domestic animal browsing ($n = 9$), which was either temporary seasonal fencing (this would preclude sheep or cattle but not native ungulates) or deferred grazing for 1 or 2 years; the remainder received no site preparation ($n = 44$). Unfortunately, due to the retrospective approach and incomplete historical records, further details were lacking.

Paired-plots design

To retrospectively assess the effect of treatments on aspen regeneration, we used a paired-plots design, where a reference plot

Fig. 1. Example of an aspen regeneration study site with $n = 7$ sample plot pairs (denoted by the white dots). The white, solid line represents the original aspen stand. A portion of that stand was removed via coppice (post-treatment plots, response to treatment), whereas pre-treatment representative vegetation remains in the intact portion. Site preparation in this case was pile and burn.



(representing the pre-treatment condition) and a post-treatment plot (representing the response to treatment) were carefully chosen (Fig. 1). Reference plots were located randomly on aerial photos within the unharvested portion of the aspen stand, and care was taken to avoid any obvious inconsistencies with the surrounding stand conditions. Post-treatment plots were selected by entering the treatment unit a minimum of 50 m from the edge of the stand while attempting to hold possible influential physiographic attributes (e.g., slope, aspect, and elevation) constant to those of the paired reference plot. Paired plots were located at least 50 m from one another in a treatment to minimize potential spatial autocorrelation and maximize within-stand variability in overstory conditions. Paired plots were located in 17 geographically distinct aspen regeneration treatments where the number of paired plots at each treatment varied (from 3 to 12) according to the area remaining in the residual stand (from ~1 to >20 ha). Given substantial observed stand-level heterogeneity, each plot pair was considered an individual sample ($n = 100$; see Statistical approach below).

In the reference stands, a 78.5 m^2 fixed-area plot was used to quantify overstory trees >10 cm in diameter at breast height (DBH, 1.3 m), which were measured for DBH, height, and height to base of the live crown; species and status (dead or alive) were also noted (Table 1). A spherical densiometer was used to obtain the percentage of canopy closure and to assign a qualitative condition to the stand (pure, pure declining, mixed, or mixed declining) based on composition and levels of mortality (Table 2). Two increment cores were extracted 90° apart from each live tree at breast height. Sapwood was reliably discerned from the heartwood in the field by holding the core to light and marking on the cores with an indelible pen. In the post-treatment plots, overstory data were measured only when the treatment did not completely remove the overstory ($n = 17$). Physiographic conditions (i.e., slope, aspect, and elevation) were measured for each paired plot.

Regeneration and understory conditions (all trees <10 cm DBH) were assessed on all reference and post-treatment plots using a 19.6 m^2 fixed-area plot. Heights and species were recorded for all trees in the plot. Advance reproduction was calculated as density per hectare and included understory stems that putatively existed prior to the treatment, whereas regeneration was defined as post-harvest stem density per hectare (the dependent variable). Because ungulate pressure within the study area has been well documented, we also quantified recent browsing activity. The browse status of aspen terminal buds (browsed or unbrowsed) was noted in the field for every aspen stem on the plot.

Factors influencing aspen regeneration

Potentially important predictors that characterize stand structure and composition were calculated from the reference plots and included total and species-specific quadratic mean diameter and basal area. After mounting and sanding per standard protocols (Stokes and Smiley 1968), increment cores were used to determine stand ages and site index (Edminster et al. 1985) and to calculate the most recent 10 year mean radial increment and aspen sapwood cross-sectional area, which are all indicators of stand vigor (Table 1). We also quantified the number of aspen cohorts, percent canopy cover of aspen, and advance reproduction of aspen and all species from the reference plots. In addition, we included slope, aspect, elevation, treatment size and type, site preparation type, ownership, and stand condition in the models (Tables 1 and 2). From the post-treatment plots, we included the density of regenerating stems, density of aspen regeneration, and an index of herbivore pressure, calculated as the ratio of browsed aspen stem density to total aspen stem density. We specifically included treatment year as a proxy for the effect of both varying climatic and time since disturbance on regeneration. To detect possible pseudoreplication among the 100 paired plots, we included a stand identification variable for the 17 distinct treatment units.

Statistical approach

The retrospective approach in this study led to an unbalanced design among many variables such as regeneration treatment and site preparation; therefore, we employed nonparametric statistical

Table 1. Summary statistics of quantitative variables.

Variable	Minimum	Maximum	Mean	Standard deviation
Reference plots				
10 year mean radial increment (mm)	2.73	16.21	7.85	3.89
Site index	35	66	50	8.4
Treatment unit size (ha)	5.0	200.0	66.91	49.30
Aspen cohorts	1	2	1.32	0.47
Elevation (m)	2429	3082	2809	204.86
Slope (degrees)	0.0	45.0	6.4	9.21
Canopy closure (%)	18.75	100.0	80.06	18.19
QMD (cm)	0.0*	47.5	22.55	9.53
Aspen QMD (cm)	0.0*	47.5	18.48	10.72
Basal area (stand, $m^2 \cdot ha^{-1}$)	0.0*	102.8	35.61	21.47
Basal area (aspen, $m^2 \cdot ha^{-1}$)	0.0*	83.89	24.94	19.38
Sapwood cross-sectional area (aspen, $m^2 \cdot ha^{-1}$)	0.0*	46.68	12.85	10.23
Sapwood cross-sectional area (stand, $m^2 \cdot ha^{-1}$)	0.0*	50.69	17.11	10.95
Advance reproduction (aspen)	0.0	45860	4096	6234
Advance reproduction (conifer)	0.0	16300	2038	2831
Post-treatment plots				
Conifer regeneration	0.0	4586	566	1091
Aspen regeneration	0.0	103900	7454	14574
Herbivory index	0.0	1.0	0.60	0.38

Note: An asterisk (*) indicates that six pre-treatment overstory plots contained no live overstory trees. QMD, quadratic mean diameter.

Table 2. Qualitative predictors of aspen regeneration.

Variable	Description
Management	The silvicultural treatment implemented; prescribed fire (n = 4), conifer removal (n = 4), removal of declining and (or) dead overstory (n = 9), complete overstory removal (n = 83)
Treatment year	Calendar year in which silvicultural treatment was implemented; 2001–2012
Site preparation	Site preparation implemented to encourage aspen regeneration after initial management (i.e., broadcast burn (n = 25), pile and burn (n = 22), domestic animal relief (n = 9), no site preparation (n = 44))
Ownership	Private (n = 43) or public (n = 57) ownership
Stand condition	Evaluation of the stand condition regarding overstory composition; i.e., pure (n = 7), pure declining (n = 16), mixed (n = 48), and mixed declining (n = 29). Stands were deemed declining if >50% of aspen overstory was dead

models to explore the relationships among variables. To quantify the drivers of post-harvest aspen regeneration, we used nonmetric multidimensional scaling (NMS), an ordination technique that is used to find structure in complex, nonparametric data (Clarke 1993). Twenty-five plot-level variables (Tables 1 and 2) measured on the 100 sample plots constituted the primary matrix in our NMS analysis. The Sorensen distance measure was used for a total of 500 runs, and stability was assessed with a plot of stress versus the number of iterations. Highly correlated variables were overlain on an ordination joint plot. PC-ORD was used to conduct NMS and display output (McCune and Mefford 2006).

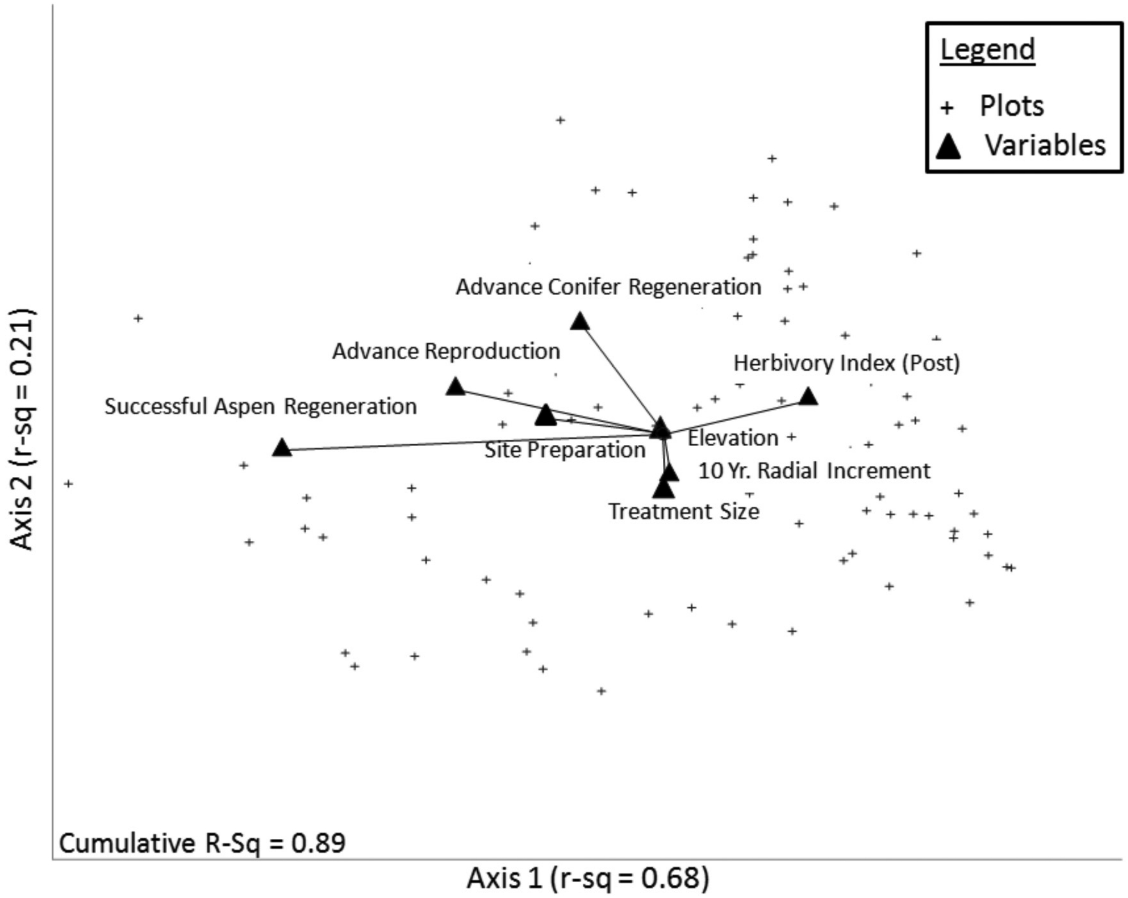
We tested the predictability of post-harvest aspen regeneration, as well as the relative importance of the predictors using random forests (RF) (Cutler et al. 2007). Advantages of RF include high classification accuracy, determination of relative variable importance, ability to model complex interactions among predictor variables, and statistical flexibility (Cutler et al. 2007). We used five classification accuracy parameters: (*i*) percentage of correctly classified observations (PCC); (*ii*) specificity, the percentage of regeneration failures correctly classified; (*iii*) sensitivity, the percentage of sites with regeneration that were correctly classified; (*iv*) Kappa (K), a measure of agreement between predicted presences and absences with actual presences and absences corrected for agreement that might be due to chance alone; and (*v*) area under the curve (AUC), the area under the receiver operating characteristic (ROC) curve. Ten-fold cross-validation was used to evaluate model accuracy. A variable importance plot and partial dependence plots were constructed to aid in the visualization of these relationships. The variable importance plot indicated the relative importance of a given predictor variable on aspen regeneration in terms of the effect of the variable on prediction accuracy. RF analysis was conducted using the randomForest package in R (R Development Core Team 2008).

Results

The NMS ordination produced a two-dimensional solution with a final stress of 13.35 (instability < 0.001; Fig. 2). Seventy-one iterations were required to reach stability (maximum = 500). Monte Carlo test results indicated that the two-axis solution was significant (P = 0.004) and explained a large majority of the variability in the data set (axis 1, r^2 = 0.68; axis 2, r^2 = 0.21; total r^2, 0.89; orthogonality, 97%; Fig. 2). There was no effect of silvicultural regeneration method (management) on aspen regeneration (Fig. 3; Table 3). However, site preparation was significantly and positively related with the first axis and browsing pressure was strongly related to axis 2 (Table 3).

Although not typically associated with vigor, advance reproduction provided a positive indication of regeneration potential among the study sites (Fig. 2; Table 3). Advance reproduction in the reference plots was less strongly related to axis 1 but was nonetheless positively aligned with aspen regeneration (Table 3).

Fig. 2. Nonmetric multidimensional scaling results are shown in a joint plot that highlights aspen regeneration drivers within the data set. Vectors with a Pearson coefficient (*r*) value (Table 3) of > 0.5 or < −0.5 are shown in relation to plot space. Axis 1 explains variation in regeneration response where ungulate herbivory and aspen regeneration occupy the opposing extremes of the axis.



As a possible positive effect of stand vigor, the second NMS axis was positively correlated with elevation (Fig. 3; Table 3). There were also subtle differences in potential productivity as indicated by the opposite (positive) relationship of both site index and 10 year radial increment (Table 3).

Aspen regeneration and the herbivory index were nearly diametrically opposed on the first NMS axis, which indicated a strong negative influence of herbivory on aspen establishment and recruitment (Fig. 2). Time since disturbance was not significantly related to either axis 1 or axis 2 (Table 3), which not only confirmed that treatment timing had little effect on the results, but also suggested that herbivore pressure in a given area has likely been relatively consistent over the timing of the treatments measured for this study.

Consistent with the results from NMS, the RF model identified that the three most important variables on aspen regeneration were herbivory index, site preparation technique, and aspen advance reproduction (Fig. 3; Table 4). Partial dependence plots revealed the nature of the relationship among these three variables and post-harvest aspen regeneration (Fig. 4). Herbivory index had the strongest influence on aspen regeneration response and demonstrated a strong negative relationship (Fig. 4*a*). The presence of aspen advance reproduction was identified as a strong predictor, as indicated by the positive relationship to aspen regeneration (Fig. 4*b*). Site preparation technique also influenced regeneration response, where in particular, broadcast-burned plots had significantly more aspen stems per hectare (Fig. 4*c*). Other significant predictor variables that were considered important in predicting aspen regeneration included elevation and site index (Fig. 3), both possible proxies for stand vigor. Stand identification was not an important variable on aspen regeneration, which suggested that pseudoreplication of plots within stands was unlikely (Fig. 3).

Discussion

Our study clearly identified herbivory as the strongest deterrent to the establishment of successful aspen regeneration and contributes to a large body of literature that has implicated browsing pressure as a major factor influencing long-term resilience in aspen (Seager et al. 2013). Although we identified two other important predictors of aspen regeneration in response to silvicultural treatments (site preparation technique and presence of advance reproduction), both of these factors are likely to be confounded by the negative impact of herbivory for a given site. The importance of advance reproduction on aspen regeneration was an unexpected result. We are unaware of previous accounts in the literature relating the presence of advance reproduction to post-harvest regeneration quantity. We also found that elevation and site index were positive predictors of aspen regeneration but were much less important that herbivory, site preparation, and advance reproduction.

Site preparation

Contrary to our expectations for the first hypothesis, silviculture regeneration method was not important; however, results suggested that the method of site preparation exerted an important and large influence on aspen regeneration response. Sheppard (2001) previously suggested that the combination of site preparation, particularly prescribed fire (i.e., broadcast burning), and

Fig. 3. Variable importance plots for predictor variable from random forests (RF) classifications used for predicting aspen regeneration. Higher values of mean decrease in accuracy indicate variables that are more important to the classification. Variable codes are defined as follows: PostHerbIndex, post-treatment herbivory index; SitePrep, site preparation technique; AsAdvRepro, advance reproduction (aspen); TenYrRI, 10 year mean ring width; OsCond, condition of aspen overstory; AsTPHA, aspen trees per hectare; AsSapwoodXSectionalArea, aspen sapwood cross-sectional area; TotSapwoodXSectionalArea, stand sapwood cross-sectional area; AsBA, aspen basal area; PreHerbIndex, herbivory in reference plots only; PreCanopyDens, canopy density in reference plots; AsCohorts, number aspen cohorts in reference plots; ConAdvRepro, advance reproduction (conifers).

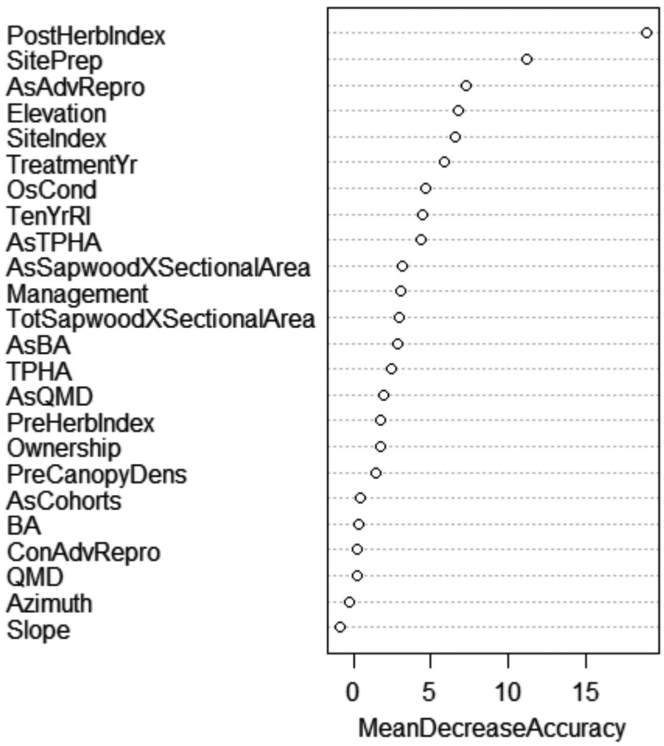


Table 3. Pearson correlation coefficients (*r*) between variables and NMS ordination axes.

	r value	
Variable	Axis 1	Axis 2
Reference plots		
Site index	0.331	−0.448
10-year radial increment	0.094	**−0.538**
Treatment size	0.043	**−0.538**
Treatment year	0.114	0.211
Aspen cohorts	0.062	−0.362
Elevation	−0.220	**0.627**
Slope	0.015	−0.191
Aspen QMD	−0.136	−0.200
QMD	−0.066	−0.046
Aspen basal area	−0.121	−0.011
Aspen sapwood area	−0.194	−0.116
Total trees per hectare	−0.159	0.274
Aspen trees per hectare	−0.180	−0.098
Total basal area	−0.019	0.217
Total sapwood area	−0.188	0.096
Advance reproduction (aspen)	**−0.608**	0.102
Advance reproduction (conifer)	−0.286	**0.553**
Herbivory index	0.340	−0.085
Canopy density	−0.182	0.316
Post-treatment plots		
Aspen regeneration	**−0.798**	−0.266
Herbivory index	**0.607**	0.425

Note: Strong response variables are in bold, i.e., $r > 0.5$ or $r < -0.5$. QMD, quadratic mean diameter.

Table 4. Metrics of accuracy for the 10-fold cross-validation of the Random Forests model.

PCC	Specificity	Sensitivity	Kappa	AUC
85.0	93.3	60.0	0.92	0.92

Note: PCC denotes the percentage of observations correctly classified, and AUC is the area under the ROC curve. Specificity is the percentage of regeneration failures correctly classified. Sensitivity is the percentage of sites with successful regeneration that were correctly classified.

associated regeneration method (e.g., harvesting) greatly benefited aspen suckering. Results from the present study suggested that broadcast burning was particularly effective at bolstering aspen regeneration numbers. This is likely because broadcast burning creates conditions conducive to aspen suckering, including the interruption of auxin flow between root and shoot segments, removal of competing vegetation, nutrient release, and increased soil temperatures. Fire also creates seedbed conditions suitable for rare, but possible, seedling establishment (Romme et al. 2005; Fairweather et al. 2014).

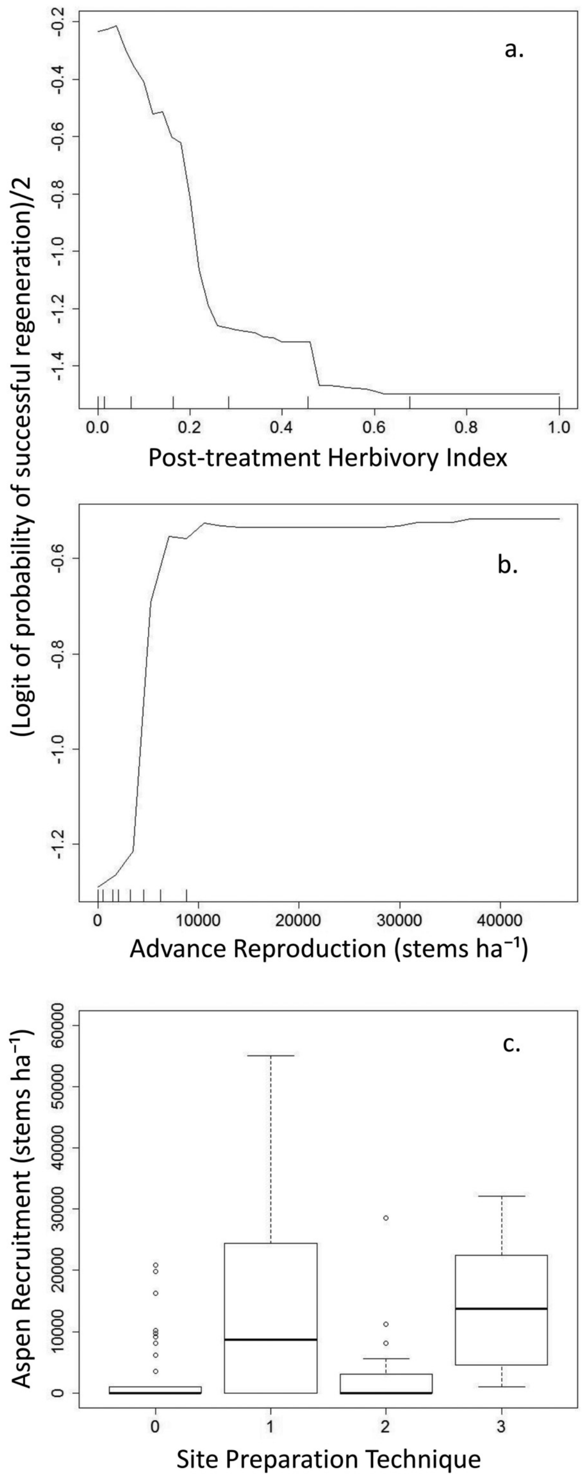
Domestic animal relief, although a less common site preparation technique, was associated with successful regeneration on seven of nine (78%) of our study sites. This was likely due to decreased herbivory pressure, primarily in the short term, which allowed aspen to achieve heights generally out of reach of browsers (i.e., >2 m). The combined results from the "no site preparation" and "pile-and-burn" alternatives resulted in poor regeneration in 59 of 66 sites (~90%). This result was likely due to a lack of stimulation of root suckering in the absence of site preparation, and pile-and-burned sites may have been subjected to excessive root damage from machinery and the burning of slash piles (Fraser et al. 2003). However, there was substantial variation in aspen regeneration across site preparation methods, including the no-treatment alternative, which resulted in aspen regeneration in a few cases.

Indicators of vigor

In support of hypothesis two, our results indicated that abundant advance reproduction, as a proxy for stand vigor, was predictive of regeneration response to treatment. The quantity of advance reproduction likely represents an integration of factors potentially contributing to successful aspen suckering response, including accumulated stand vigor, contemporary browsing pressure (or lack thereof) from herbivores, and genetic proclivity for shoot production. Aspen stands that have experienced long disturbance-free intervals can exhibit continuous regeneration (Kurzel et al. 2007), which were represented by stands with substantial aspen advance reproduction in our data set. This suggests that advance reproduction could serve as an indicator of future regeneration potential versus the possibility that advance reproduction simply imparts a direct contribution to future stocking. That is, a majority of the stands in this study were subjected to overstory removal where logging equipment (rubber-tired feller-bunchers and skidders) likely damaged most, if not all, of the advance reproduction during the harvest. Furthermore, many treatments were subject to site preparation techniques such as broadcast burning and pile and burn, which would have effectively top-killed any advance reproduction and possibly increased suckering response.

Additionally, we found that aspen sapwood cross-sectional area, the condition of overstory aspen, aspen stem density, and aspen

Fig. 4. Partial dependence plots (*a* and *b*) for variables consistently identified as important for random forests (RF) predictions of aspen regeneration. Partial dependence is the dependence of the probability of aspen regeneration on one predictor variable after averaging out the effects of the other predictor variables in the model (Cutler et al. 2007). (*c*) Raw data shown for site preparation technique. Site preparation technique codes are as follows: 0, none; 1, broadcast burn; 2, pile and burn; 3, domestic herbivory relief.



basal area were also associated with regeneration potential. Previously, poor overstory condition has been used as an indicator of "sudden aspen decline" (Frey et al. 2004; Worrall et al. 2008), with the inherent implication that a healthy overstory should relate to favorable regeneration conditions after the harvest. Also, aspen stem density and basal area have been previously identified as indicative of regeneration potential (Worrall et al. 2010; Perrette et al. 2014). The positive relationship between NMS axis 2 and elevation indicated a possible trend associated with overall stand vigor (higher elevation stands more likely to exhibited regeneration) or a trend related to ownership (lower elevation sites tended to be privately owned, whereas publicly managed sites were higher in elevation). Although these ancillary indicators of stand vigor could be taken into account when evaluating the regeneration potential of an aspen stand, our results indicated they would be secondary to site preparation, advance reproduction, and browsing pressure.

Browsing pressure

In support of hypothesis three, we found that herbivore pressure (i.e., the herbivory index) was the primary driver of aspen regeneration. This is not the first study in the region to document the negative effects of considerable browsing pressure on understory aspen (Tshireletso et al. 2010; Rogers and Mittanck 2014). The Cedar Mountain area has been previously assessed to exhibit levels of regeneration not sufficient to perpetuate the aspen type, and although herbivory was not identified as the definitive cause of reproductive failure, the possibility was acknowledged (Rogers et al. 2009). Previous research utilizing aspen enclosures and (or) exclosures has implicated browsing as a strong deterrent to aspen regeneration (Kota and Bartos 2010; Brodie et al. 2012). For example, on the Markagunt Plateau, near this study area, DeRose and Long (2010) observed the only aspen acceding to the canopy occurred on sites that had a natural herbivore exclosure (lava flow substrate). Previous work conducted in a climate similar to our study area indicated herbivore use of aspen habitat as the primary factor limiting aspen recruitment (Rogers and Mittanck 2014).

Although herbivory was the primary determinant of aspen regeneration, it likely interacted with the other factors measured in this study. For example, the quality (i.e., height) and quantity of advance reproduction is inherently dependent on antecedent herbivory in the stand and may also indicate its present impacts. Similarly, the background level of browsing pressure was likely influenced by the site preparation method. For example, domestic animal relief has obvious and direct post-treatment impacts on browsing, where less manageable native ungulate populations are not excessive. Broadcast burning may dissuade herbivores within treatment areas by removing vegetation, thus redirecting herbivores to the diverse understories of adjacent aspen stands (Coop et al. 2014).

Management implications

Inferences drawn from this study are generally limited to management in mixed and pure aspen types of the western Colorado Plateau, a region where "sudden aspen decline" and climate change type drought are prevalent (Worrall et al. 2013; Breshears et al. 2005). We strongly reiterate the recommendations of Rogers and Mittanck (2014) who suggested that pre- and post-treatment monitoring was mandatory to evaluate the appropriateness and effectiveness of regeneration treatments. Of course, post-treatment identification of the appropriate target stocking levels is necessary to evaluate the success of an aspen regeneration treatment (Long et al. 2010). Although our study indicated that herbivory is a major determinant of aspen regeneration success, there are, unfortunately, limited effective options for mitigating the detrimental impacts of browsing in practice. Because herbivory can have particularly severe negative consequences on regeneration, identifying this potential risk prior to treatment is extremely important, and we have provided a specific measure (herbivory index) for assessing browsing pressure. Herbivore damage to aspen could be significantly reduced through the use of constructed (e.g., livestock fencing, wildlife exclosures) and natural (e.g., slash debris, tree hinging) barriers. However, in practice, these measures are limited by high costs and (or) a lack of slash materials present in aspen stands. Alleviation from domestic ungulates through alteration of pasture rotation and animal stocking numbers may also be effective, when possible. If protection from herbivory is unattainable, one might consider delaying harvest until regeneration conditions become more favorable (Bartos and Campbell 1998).

Although traditional aspen silviculture has not focused on carrying over advance reproduction as a component of the future stand, we suggest it should. The presence of advance reproduction is an easy to monitor factor that our results indicate could be used to prioritize which stands to treat. Furthermore, an evaluation of the quantity and quality of advance reproduction augments the ability to forecast post-treatment regeneration, both in terms of the inherent stand regeneration potential and the current levels of herbivory. Promotion of advance reproduction in stands where it is lacking should be considered and may be achieved through opening small gaps in the overstory (Long and Mock 2012). Broadcast burning and relief from domestic animal browsing serve as the best site preparation techniques and should be seriously considered as part of any aspen regeneration treatment. Finally, it is imperative that the browse condition of regeneration be regularly monitored after treatment. In the event that browsing pressure is observed to be increasing, stems must be protected to avoid regeneration failure.

Acknowledgements

This work was funded by grants from the USU Cedar Mountain Initiative and USDA NIFA Food and Agricultural Sciences National Needs Graduate and Postgraduate Fellowship (NNF) Grants Program. Patrick Moore (USDA Forest Service) and Sarah Shaughnessy (Utah Division of Forestry, Fire and State Lands) served as extremely valuable resources, providing great assistance regarding sample site selection.

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