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Tribal and state ecosystem management regimes influence forest regeneration

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ABSTRACT

Wild ungulates such as white-tailed deer (*Odocoileus virginianus*) are highly valued wildlife assets that provide subsistence, economic and cultural benefits to hunters and rural communities. Yet, high density populations of these herbivores can contribute significantly to regeneration failures in a wide range of forest types. Pre-European settlement white-tailed deer densities were estimated to have been approximately 2–4 deer km^{-2}, and similar densities have been recommended to balance contemporary forest regeneration and wildlife objectives.

We studied northern red oak (*Quercus rubra* L.) regeneration on neighboring tribal and state forests where socio-cultural differences have led to distinct hunting management practices and subsequent differences in wildlife-plant interactions. Tribes such as the Lac du Flambeau Chippewa have kept deer populations relatively low on reservation lands through active hunting practices. We used an observational study approach to compare in situ ungulate herbivory under low (2–3 deer km^{-2}) and high (>10 deer km^{-2}) population densities. We measured northern red oak regeneration on tribal and state forests in two management unit types: contiguous stands of oak >15 ha in area and small residual “pockets” of oak <3 ha left by foresters as a source of seed and wildlife mast. Herbivory levels were significantly higher on state forests than tribal forests and were closely correlated with the density of larger seedlings, particularly in oak pockets. If herbivory levels are too high, even with adequate light, our results suggest that seedlings may not survive in densities sufficient to maintain northern red oak as a co-dominant species in mixed forests. However, when deer densities are kept at 2–4 deer km^{-2}, our results suggest that northern red oak seedlings can survive beyond browseable heights in sufficient numbers for maintaining oak. Tribal lands can provide contemporary examples of longstanding low to intermediate deer densities and sustainable deer–forest relationships.

1. Introduction

Protecting the world’s forests is becoming progressively challenging. Forests not immediately in danger of deforestation face a long list of threats to their functional integrity including elevated levels of herbivory by high density populations of ungulates and other herbivores. Forest impacts attributable to excessive herbivory include biotic impoverishment and homogenization (Rooney et al., 2004) and regeneration failures in ecologically and economically important tree species.

Oak species (*Quercus* spp.) are highly valued for timber products and as a major food source for wildlife (McShea and Healy, 2003). They also have aesthetic, cultural and ecological significance throughout the Eastern United States (US) and other temperate regions of the world (Isebrands and Dickson, 1994). Although oaks remain a common canopy component within a variety of mixed forest types, for the last several decades understory oak seedlings have been failing to survive and transition to the overstory canopy at sufficient rates to maintain their dominant and co-dominant status (Lorimer, 1992; Palmer et al., 2004). A long list of potentially interacting factors including fire suppression, excessive herbivory, damage by forest insects and pathogens, understory competition and inadequate light resources have been linked to the decline of oak forests (Abrams, 2003; Lorimer, 2003), but clear understanding of these underlying issues and proven strategies for oak forest management remain elusive (Crow, 1988, 1992; Lorimer, 2003).

White-tailed deer (*Odocoileus virginianus*) and other large ungulates have been implicated for regeneration failures among oaks and other tree species (see reviews by Gill, 1992; Côté et al., 2004; Wisdom et al., 2006). When deer populations reach high densities, their herbivory has been shown to severely affect forest regener-

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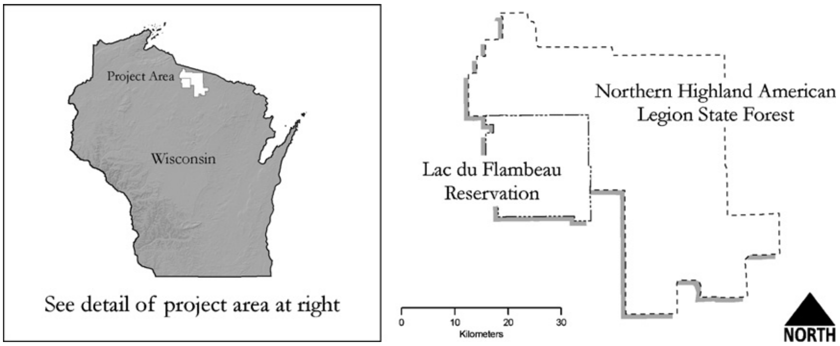

Fig. 1. Map of study area and surrounding region.

ation (Frelich and Lorimer, 1985; Gill, 1992; Rooney and Waller, 2003) and alter the structure and composition of forests (Augustine and McNaughton, 1998; Rooney and Waller, 2003; Tremblay et al., 2007). Yet, white-tailed deer are highly regarded for their subsistence, recreational, and cultural values, and spending associated with recreational hunting contributes significantly to rural economies. For example, in 2006, approximately $4.6 billion was spent on trip-related expenditures (e.g., lodging, food, guide fees, etc.) by big game hunters in the U.S. (U.S. Fish and Wildlife Service, 2006). Forest and wildlife managers must therefore balance the trade-offs between a significant wildlife asset and possible ecological and economic threats posed by high deer densities.

Wildlife managers choose their management strategies based in part on the hunting culture and other cultural contexts of their constituent societies. As McCorquodale (1997) stated, "cultural contexts are extremely important aspects of hunting management; they mandate objectives and constraints within which wildlife managers must operate." On American Indian reservations where hunting is primarily a subsistence activity and per capita consumption of wild game by tribal citizens is very high, hunting is used as a primary tool for controlling game populations. By contrast, on public forestlands in the U.S., where the majority of hunters are pursuing recreation more than harvesting meat, the use of hunting to control wildlife populations such as white-tailed deer is declining (Brown et al., 2000).

Because American Indian hunters are meat-focused and readily harvest both antlered and antlerless deer, hunting pressure tends to be higher and deer populations lower on Indian reservations. This trend has been documented, for example, in the State of Wisconsin (DeBoer, 1947; Alverson et al., 1988; Rooney et al., 2000). Considering the aforementioned linkages between deer herbivory and forest development, deer density differences across tribal and public lands could lead to important differences for forest ecosystems. To date, we know of no research that has explicitly compared forest development in light of differential deer densities following long-term tribal and public resource management systems.

In the present study, we investigated the effects of management-induced differences in deer densities on northern red oak (*Quercus rubra* L.) seedling growth and survival. Our study was implemented on adjacent tribal and state forestlands in North Central Wisconsin where differing approaches to white-tailed deer management have led to distinctly different deer population densities for the last half century or longer (DeBoer, 1947; Alverson et al., 1988; Rooney et al., 2000). Deer move back and forth across this management boundary, but due to greater hunting pressure, average deer densities are significantly lower on tribal lands. Our specific research objective was to determine the influence management regime (i.e., tribal vs. state natural resource management approaches), management unit size and/or interactions between these two factors have on the growth and survival of northern red oak seedlings.

2. Materials and methods

2.1. Study site

2.1.1. Forest ecosystems

Our study site was comprised of the >35,000 hectare (ha) Lac du Flambeau (LDF) Reservation (federally recognized homeland of the Lac du Flambeau Band of Lake Superior Chippewa Indians) and the >95,000 ha Northern Highland – American Legion State Forest (NH-AL) in North Central Wisconsin (Fig. 1). Forest ecosystems on the LDF Reservation and NH-AL have similar bio-physical conditions. Climate in both areas is characterized by a 121-day growing season, average temperatures range from −6.7 to 35 °C and average annual precipitation ranges from 76.2 to 86.4 cm (Albert, 1995; internal resource management plan, LDF). Elevation ranges from 442 to 590 m. The most common physiographic systems in both sections of the study area are pitted outwash and ice contact-derived landform systems. The study area falls within one regional ecosystem called the "Lac Veaux Desert Outwash Plain" (Albert, 1995). The NH-AL and LDF Reservation have a similar mix of forest cover types with aspen types as the most abundant followed by red/white pine followed by northern hardwoods, forested wetlands and northern red oak (internal resource management plan, LDF; WDNR, 2005).

Through conversations with local resource managers plus field and GIS-based reconnaissance we determined that northern red oak grows in a diversity of sites within our study area ranging from dry, nutrient poor outwash plains alongside northern pin oak (*Quercus ellipsoidalis* E.J. Hill) to mesic sites dominated by sugar maple (*Acer saccharum* Marshall) and eastern hemlock [*Tsuga canadensis* (L.) Carr]. In our study area, northern red oak is more typically a dominant or co-dominant canopy component on intermediate quality sites associated with ice-contact and outwash plain physiographic systems.

2.1.2. Forest and wildlife management

There are noteworthy differences and similarities between natural resource management priorities on the LDF Reservation and the NH-AL; differences that are rooted in socio-cultural distinctions between state forest constituents and tribal citizens. Both land areas are managed to maintain ecosystem health and conserve biological diversity. However, on the NH-AL, managers also prioritize providing recreation opportunities for Wisconsin citizens, whereas on the LDF Reservation, subsistence hunting and gathering, preservation of culturally important plant and animal species and protection of culturally significant sites are important management priorities. The state forest serves as a public resource for all the people of the State of Wisconsin, whereas forests on the LDF Reservation are managed to meet the needs of the LDF Tribe and its approximately 3100 enrolled citizens. The tribe has to balance forest preservation with community development needs that accompany their rapidly growing reservation population, but on the NH-AL, forestland development is strictly limited.

Northern red oak is managed for similar purposes and using similar silvicultural techniques on tribal and state forests. Oak is managed as a natural component of mixed deciduous forests in the region and acorn mast is a valued food for bear, deer, wild turkey and other wildlife. Oak also serves as an important timber species and harvests provide critical revenue for tribal and state programs. Shelterwood-style harvests, where a large proportion of the overstory is removed in multiple stages, are the most common technique used by local foresters to regenerate northern red oak.

In our study area, foresters manage northern red oak within forest stands where it is dominant or co-dominant in the forest canopy. They also maintain smaller clusters of northern red oak within stands dominated by other species. For example, it is common for stands of big-tooth aspen (*Populus grandidentata* Michx) to contain small clusters of oak on tops of small hills and ridges within pitted outwash and ice-contact terrain. Tribal and state forest managers intentionally leave these "pockets" of oak intact when big-tooth aspen stands are clearcut to provide a seed source for oak expansion and as important acorn mast for wildlife. Forest managers also protect pockets of oak for similar reasons along margins of lakes, roads and wetlands. These residual pockets of oak may constitute significantly different regeneration environments for oak seedlings. First, because the oak stands have more forest interior and less edge than pockets it is possible that their light environments differ. Second, residual pockets and oak stands may represent different forms of deer habitat and the browse intensity could therefore differ.

2.1.3. *Hunting management*

White-tailed deer hunting is a popular recreational activity on the NH-AL, drawing hunters from around the state during relatively short hunting seasons in the fall and winter. For LDF tribal citizens, white-tailed deer is perhaps the most important subsistence resource (Reo, unpublished data) and they consume deer meat extensively. Lac du Flambeau tribal citizens can hunt deer year-round on the reservation, creating extensive hunting pressure on white-tailed deer. As a result, average deer densities on the reservation are consistently and significantly lower than on the NH-AL. Based on annual pellet count surveys, tribal wildlife managers have determined that white-tailed deer densities on the LDF Reservation averaged 2.6 deer km^{-2} from 1984 through 2006 (LDF integrated resource management plan, internal document). Over the same time period, based on data derived from Sex-Age-Kill methodologies, deer densities averaged 10.3 deer km^{-2} in deer management units encompassing the NH-AL (unpublished data, WDNR). Because we were unaware of any method for comparing pellet count and Sex-Age-Kill data as derived by the tribe and state in our study area, and because we were interested in the effects of deer herbivory on forest regeneration, we used a direct estimate of deer browse (see description in Section 2.2).

2.2. *Field methods*

In the summers of 2007 and 2008, with the assistance of tribal and state foresters, we identified stands for field sampling if they met the following criteria: (i) northern red oak was dominant or co-dominant in the forest canopy; (ii) a regeneration harvest (i.e., thinned sufficiently to stimulate rapid seedling growth or "release") had been implemented in the last 5–15 years; (iii) they were of intermediate site quality within the continuum of sites supporting northern red oak in the region. The first two criteria were established to limit our inquiry to sites where the potential for regeneration was not limited by either seed source or light availability. We chose to focus on intermediate quality sites where northern red oak often has a competitive advantage over more mesic species (Lorimer, 1992; Buckley et al., 1998) because these sites are becoming the focus of northern red oak management efforts in the region. We determined site quality by using ecological habitat types developed by Kotar et al. (2002). All sites were either *Pinus-Acer rubrum/Vaccinium-Aralia* (PArVAa) or *Pinus-Acer rubrum/Vaccinium* (PArV) habitat types (Kotar et al., 2002) as determined through field assessment.

We used a balanced 2 × 2 factorial design with 10 sites/study units on state and 10 on tribal forests. Further, 10 of our sites/study units were located in oak stands (5 on state and 5 on tribal forests) and 10 were in oak pockets (Appendix B). We sub-sampled each of these units using three plots. Our mixed linear modeling approach enabled us to treat plots as our primary unit of analysis, giving us a total sample size of 60 plots within 20 distinct study units. We defined northern red oak stands as any forest stand (i) that was 15 ha or larger in area, (ii) where northern red oak was a dominant or co-dominant canopy constituent and (iii) where northern red oak was a primary future management goal. We defined "pockets" for the purpose of this study as areas that (i) were less than 3 ha in area, (ii) were dominated by oak in the overstory and (iii) were an intentional part of forest management strategies, even though they were not typically delineated by local foresters as their own independent management units (i.e., stands). The oak pockets either existed as small clusters of trees within larger management units such as aspen stands or as strips of oak maintained along the margins of lakes, roads, wetlands and clearcuts.

Within selected forest stands, plot locations were determined randomly in the field, as described by Spies and Barnes (1985). All plots were at least 50 m from the outer edge of their stand to limit potential edge effects. When sampling oak pockets, for stands that contained multiple pockets of oak, we dispersed our plots among three different pockets. When sampling small elongated strips of oak along margins of lakes, roads, wetlands and clearcuts, we distributed our three plots such that they were never closer than 50 m from one another, but maintaining the 50 m edge buffer was not always feasible. General plot characteristics were sampled using a 20 m × 20 m fixed-area plot. We noted all plant species within the plot, classified the ecological habitat type using the system described by Kotar et al. (2002), recorded the number and DBH (diameter at breast height, or 137 cm) of all overstory (>10.1 cm) and understory (2.6–10.0 cm) trees by species, and described elements of site physiography including the landform type, slope, position on slope and aspect.

To document northern red oak seedling and sapling densities, we further sub-sampled our stands of interest using five circular plots (5 m diameter) in fixed locations within each plot (for plot arrangements and other details of sampling design, see Appendix B). Within these sub-plots, we counted all northern red oak seedlings in three size classes: 0–50 cm; 51–137 cm; and >137 cm. These size classes were chosen because they are easy to implement quickly in the field. We also harvested 3 seedlings within each plot to determine northern red oak growth rates (i.e., height growth per year). We were careful to select individuals that established in response to the most recent regeneration harvest or heavy thinning. When no seedlings were present within a given plot, we collected individuals from outside the plot, but always within approximately 50 m.

To estimate deer browse pressure, we modified the sugar maple browse index method of Frelich and Lorimer (1985) for use with northern red oak. We used this browse index instead of alternative measures because it accurately and inexpensively provided comparable estimates on state and tribal portions of our study area and because the data could be analyzed at the plot level. We considered replicating the pellet count survey methods used by the LDF Tribe; however this method was deemed inappropriate for establishing plot-level deer population estimates. Further, pellet count surveys have been found to be less accurate than direct count measures (Langdon, 2001) and the sugar maple browse index has been used successfully to measure the response of northern red oak seedling to browse pressure by white-tailed deer (Rooney and Waller, 2003). The sugar maple browse index quantifies browse intensity by establishing a ratio of seedlings browsed to total number of seedlings counted where only seedlings 30-200 cm in height with current growing season terminal shoot herbivory are tallied as "browsed." Seedlings below 30 cm in height are ignored to exclude small mammal herbivory from the analyses. We modified this index by limiting our counts to a slightly different size range to maintain consistency with our vegetation sampling size classes (i.e., we counted browse on seedlings in the 51–137 cm and >137 cm height classes). Also, we counted seedlings with deer browse on terminal shoots and lateral shoots/branches rather than just terminal shoots because of differences in how maples and oaks respond to herbivory. We recorded the proportion of northern red oak seedlings that were browsed vs. un-browsed along a 240 m × 1.5 m transect in a pattern that concentrated our sampling near plot locations. The deer component of our study was conducted without using fenced enclosures or exclosures because we were interested in comparing in situ deer herbivory on tribal and state forests.

Investigation of how light availability interacts with deer browse and/or management unit size to influence oak regeneration was beyond the scope of our study. We chose stands that had ample light for promoting rapid growth of oak seedlings, theoretically marginalizing the effects of light in this study. However, because light is a dominant factor influencing oak seedling growth (Crow, 1992; Johnson, 1994) and the light environment in our study plots was highly heterogeneous, we documented light availability and included it in our statistical analyses to account for influences light may have on variation in our response variables.

To estimate understory light availability, we recorded canopy openness (i.e., % of full sun) through hemispherical photograph analysis (Canham, 1988). We took canopy photos in low light conditions using a Nikon Coolpix5000 digital camera and Nikon UR-E6 180^0 fisheye lens. Canopy photos were processed using Gap Light Analyzer 2.0 software (Frazer et al., 1999).

2.3. Quantitative analyses

To examine differences in northern red oak seedling development and stand structure due to management regime and stand size, we used linear discriminant analysis (Johnson and Wichern, 2002) and linear mixed-effects analysis of variance (ANOVA, Zuur et al., 2009). Both of these techniques assume normal distribution of the input variables within treatment groups and a linear relationship between independent and dependent variables (see Pinheiro and Bates, 2000; Johnson and Wichern, 2002). We assessed the distribution of each variable using histograms and Shapiro–Wilk's normality tests (Royston, 1982) and transformed variables as necessary (Appendix A).

Density of >137 cm oak seedlings was the only variable that did not approach a normal distribution even after transformation due to the abundance of plots with zero seedlings >137 cm in height. The effect of violating the ANOVA normality assumption in this case may be an *F* statistic that is too small (Lindman, 1974) and increasing the possibility of type I error. We elected, however, to keep this variable because of its relationship to deer density and forest management in the study area despite the fact that it might make it more difficult to detect significant differences between the treatment groups. While a non-parametric statistical test could have been used for this variable, we chose to continue with the parametric ANOVA because of the nested, mixed-effects nature of the study and to maintain consistency in interpretation with the other variables.

We examined differences in stand structure related to management regime (state vs. tribal) and size of management unit (stands vs. pockets) using a linear discriminant analysis (LDA). Linear discriminant analysis finds the linear combination of input variables that best separates categories to which different observations belong (Johnson and Wichern, 2002). The independent variables used for the LDA were canopy openness, percent deer browse, total basal area, and basal area of red oak >25 cm DBH. Basal area of red oak >25 cm DBH was included as a variable because trees of this size class are expected to provide the most abundant seed source in northern red oak stands (Sander, 1990). For the LDA, these variables were rescaled to a mean of zero and a standard deviation of 1. Each plot was assigned a code for the LDA corresponding to its *management regime:management unit size* (hereafter "regime:size") combination. The linear discriminant axes were interpreted using their weighting coefficients, and the plots were graphed on the first two axes to evaluate separability by the four variables. To assess the reliability of the LDA at discriminating stands, we performed a leave-one-out cross-validation where each observation, sequentially, was left out, the LDA ran, and the regime:size combination of the missing observation predicted. The predicted and actual regime:size values for each plot were collected and used to construct an error matrix for the LDA.

To test for differences between management regime (state vs. tribal) and management unit size (stands vs. pockets) we used a 2-way ANOVA for northern red oak growth rate and density in the three size classes. We used linear mixed-effects modeling to account for the hierarchical nature of this study design (i.e., plots nested within stands) and to capture within-stand variability. Plots nested within stands were considered random effects.

Standard ANOVA requires the assumption of independence of treatment groups and equal variance of the response variable between treatment groups. The nested nature of our study design violated this first assumption, and the variances between treatment groups were not equal (as determined by an *F* test for equal variances) for any of the response variables. A mixed-effects ANOVA, however, provides for dependence between the random effects (i.e., stands and plots) and also for variance to be different between treatment groups (Pinheiro and Bates, 2000).

To test for differences in our response variables (oak seedling growth rate and oak seedling densities in three height classes), we used separate, hierarchical two-way ANOVAs for each response variable including the following as covariates: canopy openness, percent deer browse, total plot basal area (i.e., area occupied by the cross-section of tree trunks at a height of 1.37 m), and basal area of northern red oak >25 cm. Regime (tribal vs. state) and size (pockets vs. stands) were the ANOVA fixed effects. For each response variable, we constructed multiple models with different combinations of the fixed effects, covariates, and their two-way interactions and selected the model with the lowest Akaike Information Criteria (AIC, Burnham and Anderson, 2002). In each case, the best model included the main fixed-effects of regime (state vs. tribal) and size (pockets vs. stands), a two-way interaction between regime and size, with canopy openness and basal area of northern red oak >25 cm DBH as a covariates. Percent browse, total basal area and total northern red oak basal area were not significant variables in any of the models, and so were not included in the final model structure.

To test for differences between treatment groups (where each regime:size combination was considered a treatment group), we used Tukey's Honestly Significant Difference (HSD) test (Tukey, 1953; Gotelli and Ellison, 2004) with graphs of the response variables within each of our four treatment groups to help interpret the results.

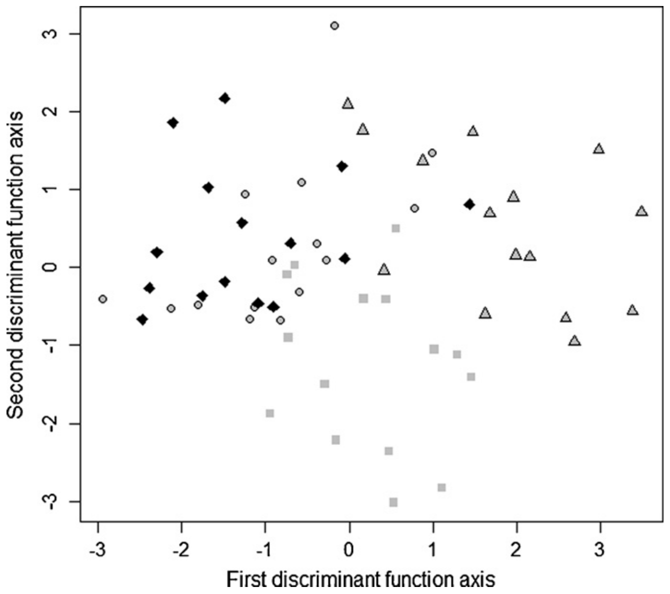

Fig. 2. Plot of management regime and management unit size by the first two linear discriminant function axes. State pockets (gray circles) and stands (black diamonds) were very similar to each other, but were distinct from tribal pockets (gray squares) and stands (gray triangles).

3. Results

The LDA for discriminating regime:size combinations showed separability between management regimes, but little separation of management unit size within the management regimes (Fig. 2). The first two linear discriminant axes accounted for 90.7% of the variability in the data (66.3% and 24.7% for the first and second axes, respectively). The first linear discriminant axis loaded positively on canopy openness and red oak basal area and negatively on percent deer browse. We interpreted this axis as: high values for the axis had high canopy openness and red oak basal area and low percent deer browse; whereas low values on the axis had high percent browse and low canopy openness and red oak basal area (Table 1, Fig. 2). The second axis weighted heavily on all four variables, but only accounted for 24.7% of the variability in the data. Using the cross-validation procedure to predict management regime and management unit size from the original data, 66.7% of the stands were correctly classified. Percent of observations correctly classified (i.e., producer's accuracy) ranged from 53.33% for state pockets to 73.33% for tribal and state stands. Percent of predicted classes correctly assigned (i.e., user's accuracy) ranged from 57.14% for state pockets to 83.33% for tribal pockets.

Based on the role of canopy openness, percent deer browse and basal area of northern red oak >25 cm DBH in both linear discriminate axes, we conducted separate ANOVA's for each of these variables to examine their relationships to management regime and management unit size. Canopy openness was similar for oak pockets and oak stands on state lands, but significantly greater ($p < 0.0001$) between oak pockets and oak stands on tribal lands (Fig. 3A). Conversely, percent browse showed a significant difference with regard to management regime with a higher proportion of oak seedlings browsed on state forests than on tribal forests (Fig. 3B). Deer browse was similar across management unit size (i.e., between oak pockets and oak stands) in both state and tribal forests. Basal area of northern red oak >25 cm DBH was significantly greater in pockets than stands ($p = 0.0013$) with a marginally significant difference across management regime ($p = 0.0883$) (Fig. 3E).

Table 1
Coefficients of the first two linear discriminant axes for examining class separation of management regime:size groups by canopy openness, percent deer browse, total basal area, and red oak basal area. The first linear discriminate axis was heavily influenced by canopy openness and percent deer browse. The second axis weighted more evenly across all the variables.

Variable	Linear discriminant axis 1	Linear discriminant axis 2
Canopy openness	0.7397	0.7562
Percent deer browse	−1.1294	0.9152
Total basal area	0.1265	0.6315
Red oak basal area	0.6762	−1.5103

The ANOVA of northern red oak sapling growth rate suggested a significant interaction between management regime and management unit size ($p = 0.009$, Table 2, Fig. 4A). Pairwise comparisons between all treatment group combinations in the growth rate ANOVA indicated that tribal pockets had significantly higher growth rates than tribal stands (i.e., partial size effect, $p = 0.021$) and state stands had significantly higher growth rates than tribal stands (i.e., partial management regime effect, $p = 0.005$) at the $\alpha = 0.05$ level (Table 3). For growth rate, the random effects of plots nested within management units accounted for 47.45% of the observed variability.

The ANOVA for density of 0–50 cm northern red oak seedlings also indicated a significant regime:size interaction ($p < 0.001$, Table 2, Fig. 4B). Although each of the pairwise group comparisons showed statistically significant results (Table 3) at the $\alpha = 0.05$ level, the most significant differences were in the greater number of seedlings in pockets vs. stands on state forests ($p < 0.001$) and significantly fewer seedlings in state stands vs. tribal stands ($p = 0.001$). The random effects of plots nested within management units accounted for less than 0.01% of the total variance in the 0–50 cm height class density observations.

There were no detectable differences in 51–137 cm seedling densities due to management regime or management unit size (Table 2). All pairwise comparisons were non-significant at the $\alpha = 0.05$ level and are not reported. The random effects of plots nested within management units accounted for less

Table 2
Results of analysis of variance (ANOVA) for growth rate and density of three size classes of northern red oak seedlings by management regime (state vs. tribal) and management unit size (stands vs. pockets). Canopy openness and basal area of red oaks >25 cm DBH were used as covariates. Degrees of freedom were 1 and 40 for each *F* test.

	F-value	*p*-value
Growth rate		
Mgmt unit size	2.659	0.111
Mgmt regime	4.100	0.050
Canopy openness	0.254	0.617
Red oak >25 cm basal area	0.001	0.975
Regime*Size	7.671	0.009
0–50 cm oak seedling density		
Mgmt unit size	0.037	0.845
Mgmt regime	0.837	0.366
Canopy openness	0.079	0.379
Red oak >25 cm basal area	3.082	0.087
Regime*Size	26.242	<0.001
51–137 cm oak seedling density		
Mgmt unit size	0.003	0.961
Mgmt regime	1.366	0.245
Canopy openness	7.984	0.007
Red oak >25 cm basal area	0.539	0.467
Regime*Size	0.091	0.764
>137 cm oak seedling density		
Mgmt unit size	0.050	0.825
Mgmt regime	35.917	<0.001
Canopy openness	1.751	0.193
Red oak >25 cm basal area	4.658	0.037
Regime*Size	2.234	0.143

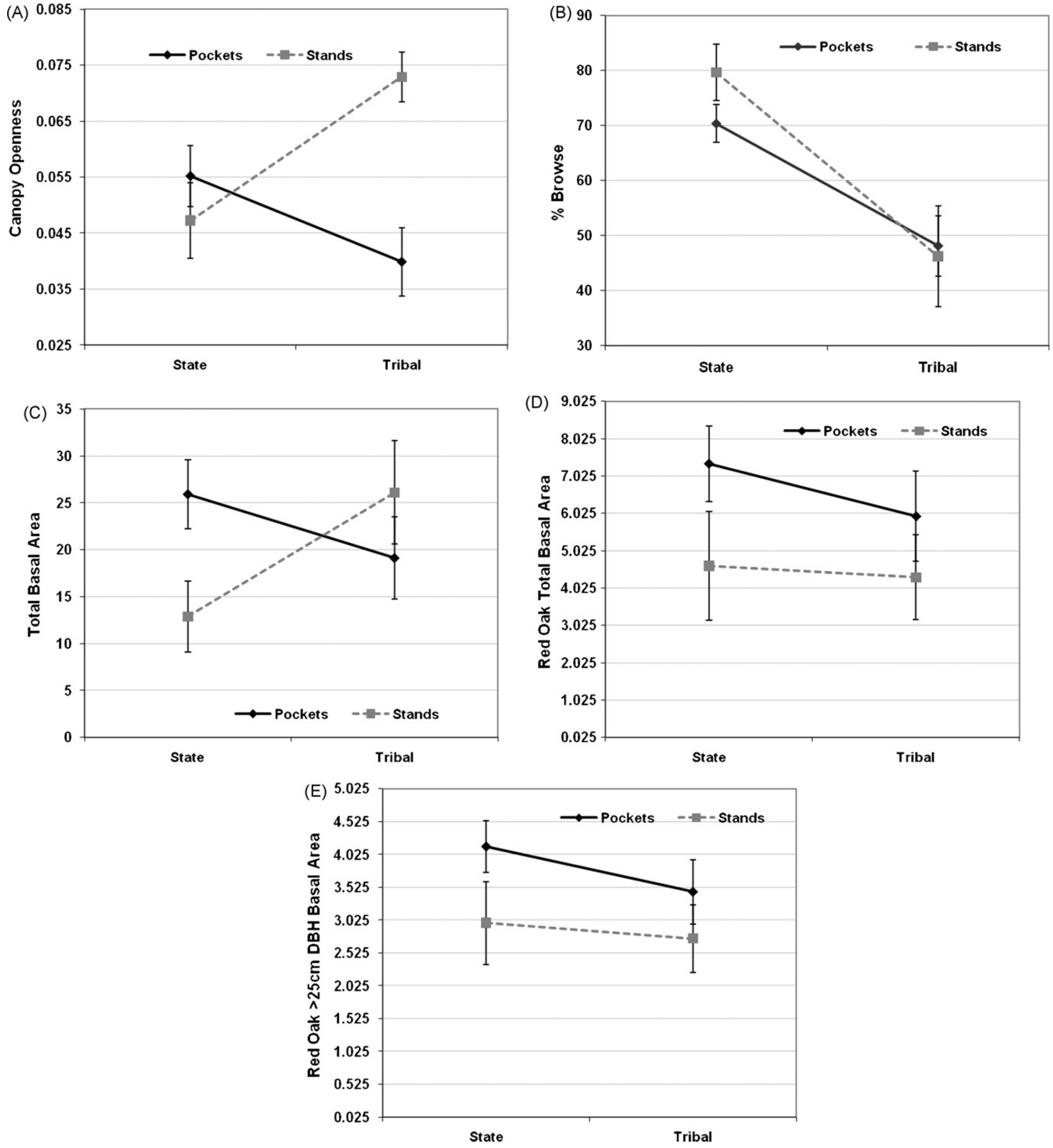

Fig. 3. Mean values for the covariates by management regime (state vs. tribal) and size (pockets vs. stands) for: (A) canopy openness, (B) percent of 51–137 and >137 cm sized oak seedlings browsed by deer, (C) total tree basal area, (D) red oak basal area, and (E) basal area of red oaks with >25 cm DBH. Variables were transformed as per Appendix A. Error bars represent 95% confidence intervals.

than 0.01% of the observed variability in 51–137 cm seedling density.

The ANOVA for density of >137 cm oak seedlings showed significantly greater seedling densities on tribal vs. state forests (Fig. 4D, $p < 0.001$). Closer examination of the significant management regime difference through pairwise comparisons indicated that the management regime effect was driven by the higher density of >137 cm oaks in tribal vs. state pockets ($p < 0.001$, Table 3). Our results also suggested a higher number of >137 cm oaks on tribal stands compared with state stands, but this difference was not significantly different (Table 3, Fig. 4D) at the $\alpha = 0.05$ level. Random effects of plots nested within stands accounted for 1.94% of the observed variation in >137 cm seedling density.

4. Discussion

This research project provides a unique contribution because we compared deer–forest relationships in the context of high deer densities, similar to those found throughout much of the range of white-tailed deer, and low deer densities that match popula-

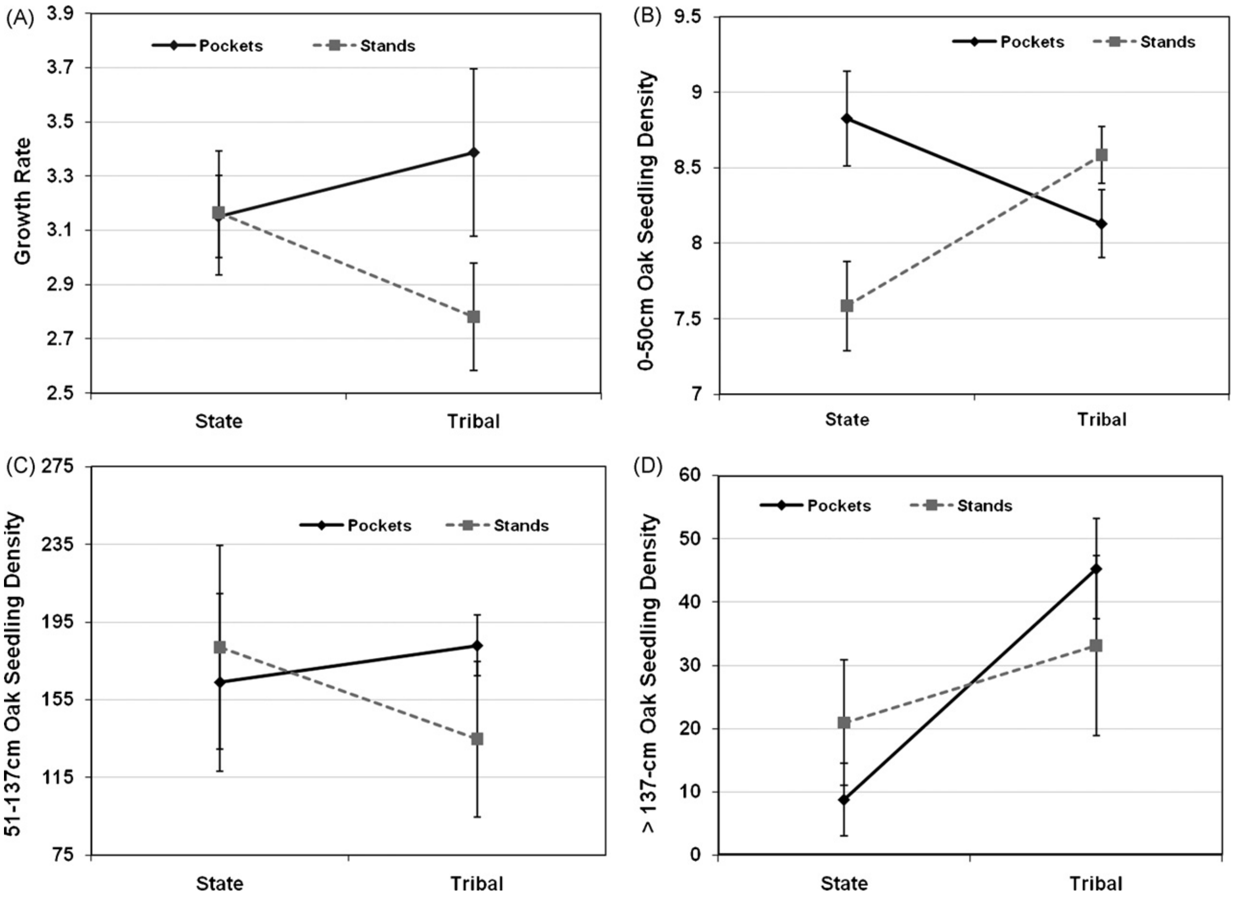

Fig. 4. Graphs of mean values for each of the four response variables (transformed as per Appendix A) by management regime (state vs. tribal) and size (pockets vs. stands) for: (A) growth rate of northern red oak seedlings, (B) density (# seedlings per ha) of 0–50 cm northern red oak seedlings, (C) density (#seedlings per ha) of 51–137 cm northern red oak seedlings, and (D) density (# seedlings per ha) of >137 cm northern red oak seedlings. Error bars represent 95% confidence intervals.

tion goals suggested by many ecologists and ecosystem managers. On tribal lands, where average deer densities are maintained at 2–3 km^{-2}, northern red oak seedlings are regenerating successfully. Our >137 cm seedling density results provide evidence regarding regeneration success or failure because these seedlings are tall enough that they are no longer browsed by white-tailed deer and therefore provide a measure of deer herbivory survival. In our study area, oak seedlings survived into this taller height class in significantly greater densities on tribal than state forests, regardless of management unit size. This result suggests that when deer densities are kept at 2–3 km^{-2}, and given sufficient understory light, resource managers can successfully regenerate northern red oak. This is a noteworthy finding given the widespread hardwood regeneration failures reported elsewhere. For this >137 cm seedling height class, seedling density (number of seedlings/ha) was more highly correlated with percent browse ($r = -0.353$) than canopy openness ($r = -0.073$) (Fig. 5) suggesting further that herbivory played an important role in determining northern red oak seedling survival in this study.

Table 3
Results Tukey's HSD test of pairwise comparisons between treatment groups for growth rate and density of 0–50 cm and >137 cm sized northern red oak seedlings. Est. diff. is the estimated difference between the treatment group means.

Comparison	Est. diff.	Std. error	*z*-Value	*p*-value
Growth rate				
State:pockets to tribal:pockets	0.277	0.224	1.236	0.583
State:pockets to state:stands	0.029	0.099	0.289	0.991
Tribal:pockets to tribal:stands	−0.728	0.257	−2.831	0.021
State:stands to tribal:stands	−0.480	0.146	−3.269	0.005
0–50 cm oak seedling density				
State:pockets to tribal:pockets	−0.686	0.240	−2.854	0.022
State:pockets to state:stands	−1.141	0.295	−3.872	<0.001
Tribal:pockets to tribal:stands	0.755	0.233	3.242	0.006
State:stands to tribal:stands	1.210	0.265	4.565	0.001
>137 cm oak seedling density				
State:pockets to tribal:pockets	32.701	6.247	5.235	<0.001
State:pockets to state:stands	6.715	7.479	0.898	0.799
Tribal:pockets to tribal:stands	−13.094	11.156	−1.174	0.634
State:stands to tribal:stands	12.892	11.191	1.152	0.647

Seedlings <50 cm in height are buried by snow in the winter when white-tailed deer do most of their woody plant browsing (Healy, 1997). We therefore expected that 0–50 cm seedling densities were driven more by light availability and seed source than deer herbivory. (Because we did not make a detailed accounting of acorn production, our best approximation of seed source is basal area of large overstory northern red oaks >25 cm DBH.) However, examination of variable correlations indicates that percent browse, canopy openness and basal area of large overstory oaks are at most weakly correlated with densities of small seedlings in our study (Fig. 5). Total stand basal area (all species) was more strongly correlated with small seedling densities, perhaps indicating that stand management history (i.e., timing and intensity of previous harvests) was influential over seedling establishment.

Light availability is likely the most important abiotic factor influencing northern red oak seedlings growth and survival (McGee, 1968; Sander, 1990; Pacala et al., 1994; Finzi and Canham, 2000). Given Finzi and Canham's (2000) and Pacala et al.'s (1994) findings that northern red oak seedlings not only grow more rapidly with increasing light levels but also cannot tolerate the slow growth that

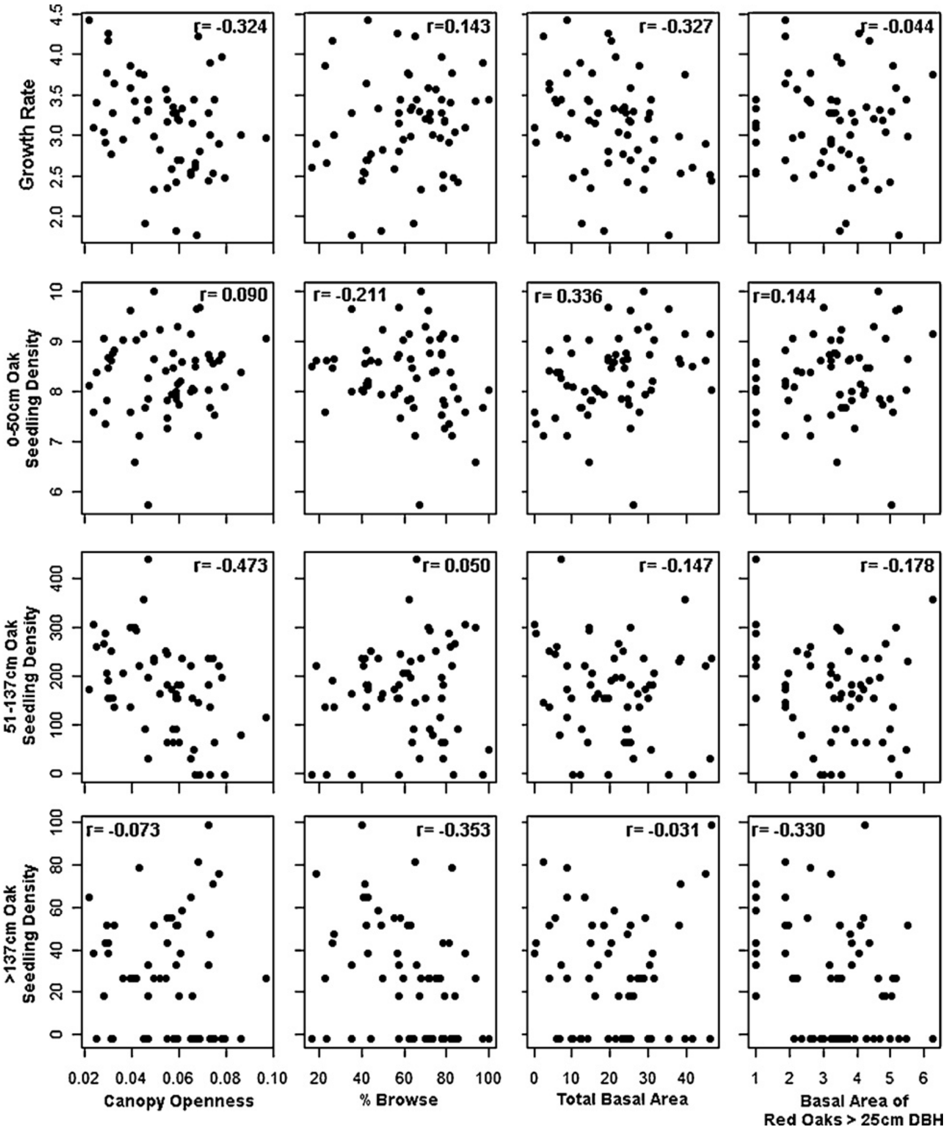

Fig. 5. Scatterplots showing correlations between each of the four response variables (transformed as per Appendix A) and four co-variates.

accompanies deep shade, adequate understory light can be thought of as a "pre-requisite" to oak seedling survival. In our study, we looked at sites that had ample light to support seedling growth and survival. Even given sufficient light, few seedlings survived beyond the browseline (i.e., low densities of seedlings >137 cm) on state forests where deer densities are high.

4.1. Management implications

In our study area, tribal natural resource management is resulting in northern red oak seedlings densities that approach silvicultural recommendations for "full stocking" (Sander et al., 1984; Wisconsin DNR, 1990). The densities of large (>137 cm) seedlings we observed on tribal lands would be more than satisfactory to most resource managers, particularly considering the struggles managers have had regenerating oak in recent decades. Seedling survival was nearly threefold greater in tribal stands than state stands and more than eightfold greater in tribal pockets than state pockets. Our results from state lands suggest that even when the prerequisite of adequate light is met, if herbivory levels are too high, seedlings may not survive in densities sufficient to maintain northern red oak as an important component of future forests. However, when deer densities are kept at 2–4 km^{-2}, northern red oak seedlings may survive in sufficient numbers for maintaining oak.

Because tribal citizens continue to use large game as a primary subsistence resource, tribal resource managers are able to use hunting as a means of achieving relatively low deer densities. For example, the deer densities maintained on the Lac du Flambeau Reservation are similar to estimated pre-European settlement densities (McCabe and McCabe, 1997) and fall within a population density range that has shown no adverse effects on forest vegetation (Augustine and deCalesta, 2003). The Lac du Flambeau Reservation provides a contemporary example of longstanding low to intermediate deer densities and sustainable deer–forest relationships. Managers of public lands, such as the Wisconsin DNR, are not able to replicate tribal hunting management programs because their work is situated in significantly different socio-cultural and political contexts. However, to sustain wildlife and forest assets, managers of public lands will need to find their own context-appropriate mechanisms for reducing deer densities.

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Appendix A.

Description of variables used in this study. The transformations that were applied to each variable so that its distribution approximated a normal distribution and the Shapiro–Wilk test for normality (null hypothesis was that the data were normally distributed).

Variable	Description	Transformation
CanOpen	Covariate measuring the percent openness of forest canopy (inverse of canopy closure)	Inverse
% Browse	Covariate measuring percentage of oak seedlings browsed by white-tailed deer	None
Total Basal	Total basal area of all trees	None
RO_Basal	Proportion of the total basal area made up by red oaks	(RO_Basal)$^{0.69}$
GrwRate	Response variable measuring average height accrued per year (cm yr^{-1}) in oak seedlings	Log
0–50Dens	Response variable measuring number of seedlings 0–50 cm in height per hectare (extrapolated from plot data)	Log
50–137Dens	Response variable measuring number of seedlings 50–137 cm in height per hectare (extrapolated from plot data)	(50–137Dens)$^{0.66}$
137 cm + Dens	Response variable measuring number of seedlings >137 cm in height per hectare (extrapolated from plot data)	Box-Cox(137 + Dens, $\lambda = 0.5$)
Mgmt regime	Fixed-effect variable with levels: state and tribal	N/A
Mgmt unit size	Fixed-effect variable with levels: oak stand and oak pockets	N/A
Mgmt unit	Random-effect variable. Management units within each treatment group numbered consecutively from one to five.	N/A
Plot	Random-effect variable. Plots within each management unit (i.e., oak stands and oak pockets) numbered from one to three	N/A

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.05.030.

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