



Research article

## Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape

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### Abstract

Landscape patterns of quaking aspen (*Populus tremuloides*) seedling occurrence and abundance were studied after a rare recruitment event following the 1988 fires in Yellowstone National Park, Wyoming, USA. Belt transects (1 to 17 km in length, 4 m width) along 18 foot trails were surveyed for aspen seedlings on the sub-alpine plateau of the Park, along gradients of elevation and geologic substrate, during the summer of 1996. Aspen seedling presence and density were characterized as a function of elevation, geologic substrate, slope, aspect, vegetation/cover type, presence of burned forest, and distance to nearest adult aspen stand. Presence of aspen seedlings was best predicted by the incidence of burned forest and proximity to adult aspen; aspen seedlings were only found in burned forest and were more likely to occur closer to adult aspen clones. When tested against independent data collected in 1997, the logistic regression model for aspen seedling presence performed well (overall accuracy = 73%,  $Tau_p = 0.41$ ). When present, variation in aspen seedling density at local scales ( $\leq 200$  m) was largely explained by elevation, with higher densities observed at lower elevations. At broad scales ( $> 1$  km), seedling density was a function of cover type, elevation, aspect, slope, and burn severity, with greater seedling density in more severely burned forested habitats on southerly, shallow slopes at lower elevations. Aspen seedling densities ranged from 0 to 46,000 seedlings/ha with a median density of 2,000/ha on sites where they occurred. Aspen seedlings were most abundant in the south central and southwest central regions of the park, approximately an order of magnitude less abundant in the southeast region, and nearly absent in the north central area. Establishment of new aspen stands on Yellowstone's subalpine plateau would represent a substantial change in the landscape. However, the long-term fate of these postfire aspen seedlings is not known.

### Introduction

Understanding the response of plant populations to large, infrequent disturbances is needed for predicting vegetation dynamics in disturbance-driven landscapes (Turner et al. 1998). For long-lived clonal plant species such as quaking aspen (*Populus tremuloides* Michx.), local re-establishment may be achieved either vegetatively or through seed produc-

tion. However, seed production is required for long-distance dispersal (Eriksson 1992), which is likely to be a key component of a species' ability to persist regionally with climate change. Climate-induced alterations in disturbance regimes (e.g., fire frequency and extent) may be proximal causes of ecological responses to climate change (see Graham et al. (1990) and Dale et al. (2001)). The recruitment of aspen seedlings following the 1988 fires in Yellowstone Na-

tional Park (YNP), Wyoming, USA offered a unique opportunity to examine interactions between a large, infrequent disturbance and post-fire seedling recruitment and to assess the ability of a plant population to potentially increase its range within a landscape.

Quaking aspen is the most widely distributed native North American tree species (Fowells 1965) and an important constituent of landscapes of the Intermountain West. Throughout the Rocky Mountains, aspen is a clonal species in which one or a few genetically-identical stems (ramets) arise from a common root system (Barnes 1966; Tuskan et al. 1996). Although aspen can regenerate either by seed or through root sprouting, it is widely believed that re-establishment of aspen from seed has been extremely rare in the Rocky Mountains since the last glaciation because climatic conditions have not been suitable for widespread germination and establishment (e.g., Pearson (1914) and Baker (1925), Moss (1938), Einspahr and Winton (1976), McDonough (1985)). Genetic diversity in aspen clones in Waterton Lakes National Park, Alberta, however, suggests that seedling recruitment must have occurred during the past 10,000 years, even if very rarely (Jelinski and Cheliak 1992). Quinn and Wu (2001) also documented aspen seedlings following recent fires in southeastern Arizona, USA. The few instances of successful seedling recruitment reported in the literature lead to the speculation that there may be brief "windows of opportunity" characterized by a combination of favorable moisture conditions, an absence of competition, and the availability of suitable substrates (e.g., burned sites) (Jelinski and Cheliak 1992). Such a window occurred in YNP following the broad-scale fires of 1988 (Kay 1993; Romme et al. 1997; Stevens et al. 1999), providing an opportunity to examine spatial heterogeneity of the distribution and survival of newly established aspen and their potential for range expansion in Yellowstone.

Although aspen occupied only ~1% of YNP prior to the 1988 fires (Despain 1991), occurring almost exclusively on the low-elevation sagebrush-grasslands in northern YNP, aspen is ecologically significant because it is the only deciduous forest type present. Aspen forests support high numbers and diversity of breeding birds and other animals (DeByle 1985b; Loose and Anderson 1995; Kalcounis and Brigham 1998), and are visually striking in the fall when the foliage turns orange and yellow in color. Very few tree-sized aspen have regenerated since the early 1900s (Houston 1982; Kay 1993; Romme et al.

1995; Ripple and Larsen 2000), and the causes of the apparent decline in aspen abundance in Yellowstone and throughout the Intermountain West have received considerable discussion (Krebill 1972; Loope and Gruell 1973; Schier 1975; Olmstead 1979; Bartos and Mueggler 1981; Hinds 1985; Boyce 1989; Kay 1990; Wagner and Kay 1993; Bartos et al. 1994; Romme et al. 1995; Baker et al. 1997; Kay 1997; Crawford et al. 1998; Singer et al. 1998; White et al. 1998; Kay and Bartos 2000). However, abundant aspen seedlings were observed in 1989 across widely distributed burned areas of the Yellowstone plateau that had been previously dominated by lodgepole pine. In 1993, five years after the fires, these seedlings were still ubiquitous and locally abundant (Kay 1993; Romme et al. 1997), suggesting that a rare seedling recruitment event was in progress.

Our objectives were to explain and predict the occurrence and abundance of newly established aspen seedling populations in YNP where aspen was absent prior to the 1988 fires. Previous studies have shown that aspen seedlings are distributed patchily (e.g., Romme et al. (1997)). However, these studies have not surveyed the range of elevation, geologic substrate, and other potentially significant physical and biological determinants in YNP nor documented their relationship to variation in aspen seedling occurrence and density. If newly established seedling populations develop into aspen stands in areas previously dominated by lodgepole pine forests, the resulting fundamental changes on the landscape could have profound biologic and management implications throughout the Greater Yellowstone Ecosystem.

## Methods

### *Study area*

Yellowstone encompasses 9000 km<sup>2</sup> in the northwest corner of Wyoming and is primarily a high, forested plateau. The 1988 Yellowstone fires affected ~45% (400,000 ha) of this area (Christensen et al. 1989; Turner et al. 1994). Fires of this scale have occurred in YNP in the past, most recently in the late 1700s (Romme 1982; Romme and Despain 1989). Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) (Despain 1991). Our study focused on the subalpine forested plateau that covers most of Yellowstone and supports similar vegetation

throughout. Aspen were absent from most of the plateau before the 1988 fires. This subalpine plateau encompasses dry, infertile habitats on rhyolite substrates and more mesic, fertile habitats that occur on andesite substrates and detrital deposits. The climate is generally cool with relatively moist springs and dry summers (Martner 1986). The two most important environmental gradients controlling vegetation on the plateau relate to elevation and geological substrate (Despain 1991), with moisture generally increasing with elevation and soil fertility lower on rhyolite than on andesite and detrital substrates.

### *Field sampling*

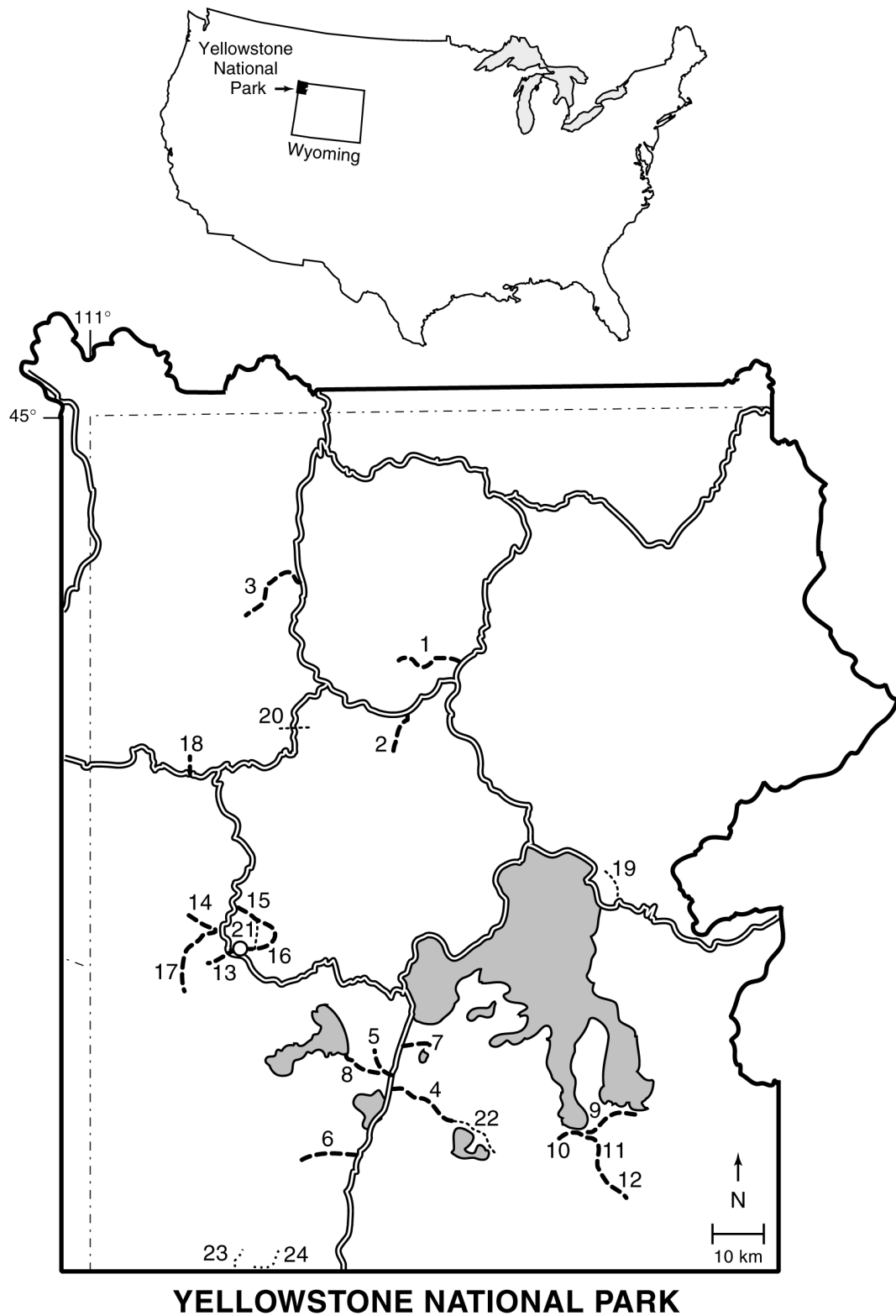
Belt transects (total of 115.1 km in length) along 18 trails (Table 1) were surveyed for aspen seedlings on the subalpine plateau in the southern, western, and north-central sections of Yellowstone National Park (Figure 1), along gradients of elevation and substrate, during July and August of 1996. We sampled primarily along secondary or unmaintained trails that are typically narrow, overgrown, and rarely traveled by people or horses. Our experience in establishing and relocating long off-trail transects in Yellowstone (Turner et al. 1997) suggested that the use of trails was the only suitable means of obtaining a spatially extensive sample in limited time. We recognized that trails typically follow less severe topography than might occur within the landscape as a whole (e.g., typically bypassing steep ravines). However, the Yellowstone Plateau is dominated by relatively gentle, undulating topography, with relatively few deep canyons or steep slopes, and the areas where trails are located are generally representative of the topography as a whole. The microenvironment adjacent to a trail also may differ from conditions off-trail, especially if off-trail vegetation is dense. However, in the burned lodgepole pine forests where we sampled, differences in wind, insolation, and plant cover between trail margins and off-trail areas appeared minor. We also sampled one off-trail transect as part of our accuracy assessment in 1997 and compared trailside surveys with 1996 off-trail estimates in other burned study plots (M. G. Turner and W. H. Romme, unpublished data), and found similar patterns in aspen density off-trail and along the nearby trail segments (see Results).

Distance along each trail was measured from the starting point with a string hipchain. Variable-length segments  $\leq 200$  m were defined as sections of trail that were relatively homogeneous in terms of vegeta-

tion or cover type, burn severity, and topography; a total of 739 segments were sampled along the 18 trails. The number of aspen seedlings occurring within 2 m on both sides of the trail was recorded for each segment, and each trail segment represented one observation in the data set. In this paper, we refer to each discrete aspen plant as a seedling, i.e., a unique genet, even though some individuals actually may have been ramets from another true seedling. However, extensive excavations and genetic analyses in three locations across the Yellowstone Plateau indicated that  $< 5\%$  of individual plants were ramets (Romme et al., submitted). We also ruled out the possibility of root sprouts from adult aspen, because we knew from extensive pre-1988 field studies in the same area (Romme and Despain 1989) that there were no adult aspen along the portions of the trails that we sampled.

The elevation (m) at the beginning and end of the segment, and the slope (degrees), aspect (degrees), vegetation/cover type, presence of burned forest, burn severity, and prominent topographic features were recorded for each segment. Elevation was obtained from digital topographic data, all other measurements were recorded directly in the field. Vegetation/cover types included forest, meadow, geyser basin, rocky surface/talus slope, and stream. Burn severity classes were unburned, light surface burn, severe surface burn, and crown fire (as defined by Turner et al. (1994)). Examples of prominent topographical features included ridge top, hill slope, valley, or undulating terrain. Slope and aspect were measured in degrees but recorded as discrete variables to minimize individual observer bias in determining these values. Slope was recorded using five classes: 0–5°, 6–10°, 11–15°, 16–20°, and  $> 21^\circ$ . Aspect was categorized by the eight subordinal-facing directions, namely north (338–22°), northeast (23–67°), east (68–112°), southeast (113–157°), south (158–202°), southwest (203–247°), west (248–292°), and northwest (293–337°).

Geologic substrate and distance to nearest adult aspen were also determined for each trail segment. Underlying geologic substrata were obtained from the Yellowstone National Park geology map (U.S. Geological Survey 1972), and were designated into four general categories: plateau rhyolite, welded ash flows, detrital deposits, and hydrothermal deposits. Distances to nearest adult aspen stands were assessed using the GRASS geographical information system (USA-CERL 1993) by plotting locations of trail seg-



*Figure 1.* Map of study area showing location of Yellowstone National Park in northwestern Wyoming, USA, and indicating locations of the trails surveyed for aspen seedlings in 1996 (dashed lines) and 1997 (dotted lines), major park roads (double lines), and major lakes (shaded dark grey). Trail numbers correspond to listing in Table 1.

Table 1. Trails along which belt transects were surveyed for occurrence of aspen seedlings in southern and western Yellowstone National Park during 1996 and 1997. Locations of trails are depicted in Figure 1 and identified by number. Data are reported for the occurrence of aspen seedlings along each trail (proportion of segments with seedlings present) and the density of aspen seedlings (mean and range).

Trail ID	Trail Name	Region of park	Elevation range (m)	Length sampled (km)	Number of trail segments	Proportion of segments with aspen present	Mean aspen seedling density (ha <sup>-1</sup> ) (range)
<b>1996 Sampling Locations</b>							
1	Cascade/Grebe/Wolf Lake	NC	2377–2438	11.5	55	0.00	0 (0–0)
2	Cygnets Lakes	NC	2485–2520	7.0	39	0.05	10.2 (0–200)
3	Mount Holmes	NW	2225–3139	17.0	71	0.17	79 (0–1200)
4	Heart Lake	SC	2316–2469	12.0	55	0.36	1,696 (0–12,393)
5	Lewis River Channel	SC	2374	0.3	2	0.50	8,247 (0–16,495)
6	Pitchstone Plateau	SC	2347–2591	9.0	29	0.21	51 (0–331)
7	Riddle Lake	SC	2410–2430	3.7	16	0.31	2,816 (0–20,000)
8	Shoshone Lake	SC	2377–2438	7.0	37	0.51	612 (0–10,000)
9	Trail Creek	SE	2375–2400	7.0	46	0.19	171 (0–2133)
10	Outlet Creek	SE	2347–2438	4.3	34	0.35	301 (0–3711)
11	Two Ocean Plateau spur	SE	2355–2455	2.5	17	0.12	48 (0–625)
12	Two Ocean Plateau	SE	2455–2645	8.0	50	0.10	24 (0–461.5)
13	Fern Cascades	SWC	2256–2316	2.9	20	0.75	7,730 (0–26,450)
14	Little Firehole Meadows	SWC	2360–2515	3.7	40	0.40	1,853 (0–30,000)
15	Mallard Creek	SWC	2256–2499	11.0	148	0.52	4,256 (0–46,700)
16	Mallard Lake	SWC	2235–2460	5.2	33	0.33	874 (0–7740)
17	Summit Lake	SWC	2225–2591	8.0	39	0.51	2,191 (0–20,000)
18	Harlequin Lake	WC	2073–2103	1.0	8	0.38	1,655 (0–10,000)
<b>1997 Sampling Locations</b>							
19	Turbid Lake Trail	EC	2378–2414	2.5	13	0	0 (0–0)
20	Monument Geyser Basin	WC	2196–2424	1.9	16	0.12	16 (0–125)
21	Mallard Creek-off trail	SWC	2256–2350	2.9	13	0.92	624 (0–2,838)
22	Trail Creek-Heart Lake	SE	2165–2190	3.6	31	0.68	142 (0–721)
23	South Pitchstone Plateau	SW	2164–2332	3.7	25	0.76	1,679 (0–6,037)
24	Beulah Lake	SW	2058–2213	5.9	31	0.84	278 (0–2,607)

\* Region = region of Yellowstone National Park; NC = north central, NW = northwest, SC = south central, SE = southeast, SWC = southwest central, WC = west central

ments and adult aspen stands and calculating the minimum distance to any adult aspen stand for each trail segment. We used digital vegetation maps for YNP (Despain 1991) that included extensive adult aspen in northern YNP and along the western border of the park, but we supplemented these distributions by mapping additional aspen stands via an aerial flight over the Park in September 1996. During the summer of 1996, we had noted the occurrence of multiple small clumps (several trees to  $\sim 0.5$  ha) of adult aspen on the subalpine plateau that were previously undocumented on the Park vegetation map. These were found mainly on isolated cliffs and talus slopes where coniferous forest was sparse or absent. Therefore, we flew over the plateau in September 1996 when the yellow leaves were highly visible and could be easily distinguished from the dominant conifers. In addition, we included the extensive aspen stands located to the west, south and southwest on National Forest lands. Distances were calculated from the final map that contained all known aspen within and adjacent to our study area.

During the summer of 1997, we censused aspen seedlings along five new trails and one off-trail transect (Table 1) to assess the accuracy of the logistic regression model describing aspen seedling presence (described below). The same sampling protocols used in 1996 were used in 1997. Trails were chosen to represent locations where aspen were expected to be present or absent based on a spatial extrapolation of the logistic regression analysis. A total length of 37.2 km including 129 trail segments was sampled in 1997.

#### *Data analyses*

Variation in aspen seedling presence as a function of the set of independent variables (Table 2) was examined using stepwise forward logistic regression (SAS Institute, Inc. 1989). Logistic regression explicitly assumes binomially distributed errors and is appropriate for modeling the effects of discrete and continuous variables on discrete dependent variables such as presence/absence (Trexler and Travis 1993). We used the logit model (Trexler and Travis 1993) and fit the logit by using a maximum likelihood method. Adequacy of all logistic regression models was assessed by the significance of the parameters in explaining variation (likelihood ratio Chi square test and Wald's test) and the fit of the predictions to data (goodness-of-fit with percent concordance reported and testing

with independent data as described below). Two types of analyses were performed. First, aspen density data were categorized as aspen present (1) or aspen absent (0), and the probability of aspen being present was modeled. Second, to examine areas of high aspen density, the data were categorized into three groups: aspen absent, low-density aspen ( $0 < x < 2000$ ), and high-density aspen ( $\geq 2000/\text{ha}$ ). The density of 2000/ha was the median density for the segments at which aspen were present. Logistic regression simultaneously modeled the probability of aspen being present at low and high densities, and generated parallel equations predicting the probability of occurrence of each.

Because the regression analyses required all independent variables to be continuous, several were reclassified as ordinal dummy variables (Table 2). Presence of burned forest was designated as 0 for unburned forest and 1 for burned forest. Burn severity classes (Turner et al. 1997, 1999) were ordered to increase with burn severity, from zero for unburned to three for crown fire. Aspect was categorized in ascending order from northerly to southerly. Slope was scaled from 1 (flat) – 5 (steep). Cover type was classified such that tree cover increased with ordinal value: (1) rocky talus and geyser basin, (2) meadow, (3) stream-side, and (4) forest. Geologic substrate was ordered to increase with fertility (Table 2).

For trail segments in which aspen seedlings were present ( $n = 235$ ), variation in aspen density at these fine scales (trail segments were all  $\leq 200$  m) was modeled as a function of the set of independent variables (Table 2) using stepwise multiple regression (SAS Institute, Inc. 1989). Density data were log transformed prior to analysis to achieve normality. Seedling density data were also tested (using S + SpatialStats) for spatial autocorrelation among trail segments using correlograms estimated for 20 lag distances on each trail, unless there were too few observations (Kaluzny et al. 1998). Correlogram results demonstrated no major or consistent spatial autocorrelation in the data structure. For most trails,  $r$  varied about zero, with an occasional  $r \sim 0.4$ . Results of best subsets regression identified which variables were significant in explaining variation in aspen density, as well as the relative contribution (partial  $r^2$ ) of each significant variable to the explanatory power of the model.

To address broad-scale ( $> 1$  km) patterns of variation in aspen seedling density, mean values for each variable were calculated for each trail, resulting in a

Table 2. Summary of independent variables and ordinal dummy variables used in regression models to predict aspen occurrence and density in Yellowstone National Park. See Methods for details.

Variable	Levels	Source
Presence of burned forest	(0) Unburned, (1) burned	Recorded in field; obtained from interpreted Landsat data (Turner et al. 1994) for extrapolation
Burn severity	(0) Unburned, (1) light-surface burn, (2) severe-surface burn, (3) crown fire	Recorded in field
Slope	Degrees, categorized as: (1) 0–5°, (2) 6–10°, (3) 11–15°, (4) 16–20°, and (5) > 21°	Recorded in field
Aspect	Degrees, categorized as: (1) northerly, 293–360° and 0–67°; (2) easterly and westerly, 68–112° and 248–292°; and (3) southerly, 13–247°	Recorded in field
Elevation	Beginning and end elevation (m) for each segment used to compute mean	Determined from GIS and 7.5' topo maps
Distance to adult aspen	Continuous (km)	Computed in GIS from park vegetation map supplemented by mapping from aerial photography
Vegetation/cover type	(1) Rocky/talus and geyser basin, (2) meadow, (3) streamside, (4) forest	Recorded in field
Geologic substrate	(1) Ash flows, (2) hydro-thermal deposits, (3) rhyolite, (4) detrital deposits	YNP Center for Resources, GIS coverage

Table 3. Results of logistic regression analyses (analysis of maximum likelihood estimates) predicting (a) presence of aspen seedlings along trail segments ( $n = 739$ ), and (b) presence of low ( $\leq 2000$  stems  $\text{ha}^{-1}$ ) and high ( $> 2000$  stems  $\text{ha}^{-1}$ ) density aspen seedlings as a function of the independent variables. The latter model estimates parallel lines having different Y intercepts.

(a) Concordance = 75.6%				
Variable	DF	Parameter estimate	Wald $\chi^2$	Pr > $\chi^2$
Intercept	1	-1.36	9.05	0.0026
Distance from mature aspen	1	-0.17	71.90	0.0001
Burn class	1	2.52	32.76	0.0001
(b) Concordance = 77.3%				
Variable	DF	Parameter estimate	Wald $\chi^2$	Pr > $\chi^2$
Intercept (low density)	1	-1.7758	0.1758	0.6750
Intercept (high density)	1	-0.6739	0.025	0.8736
Burn severity class	1	0.8604	44.97	0.0001
Elevation	1	-0.0038	18.42	0.0001
Distance from mature aspen	1	-0.039	15.71	0.0001
Geologic substrate rank	1	-0.3675	7.22	0.0072
Cover class	1	2.177	5.50	0.0190

data set with 18 observations. All trail segments were used to compute the mean (i.e., including segments in which no aspen occurred), and a square-root transform was applied to the density data to achieve normality prior to analysis. Mean aspen density was modeled as a function of the set of independent variables using best subsets multiple regression (SAS Institute, Inc. 1989) as described for the fine-scale analysis.

Finally, we produced a spatially explicit prediction of aspen seedling occurrence for unsampled trails across the Yellowstone landscape using the equation from the logistic regression model in a geographical information system. The applicable data layers from the GIS (e.g., elevation, distance to nearest aspen, and presence of burned forest) were obtained using 50-m grid cells, and the regression equation was used to predict the probability of occurrence of aspen seedlings. This map was used to identify new areas in which aspen seedlings were sampled during the summer of 1997 to test the model. Prediction accuracy was then assessed as follows. A given trail segment was predicted to contain aspen seedlings if the probability of aspen presence obtained from the model was  $\geq 0.50$ . Predicted and observed presence of aspen seedlings were then compared for each new trail segment, and overall agreement was determined by computing the percentage of correct predictions (correct presence + correct absence / total). Second, a two-way contingency matrix was constructed con-

trasting observed values of aspen seedling occurrence with predicted occurrence for all new trail segments. This table was evaluated using the  $\text{Tau}_p$  statistic, which quantifies the improvement in a model's predictive power over a random assignment of values to cells (Ma and Redmond 1995).

## Results

### *Aspen seedling presence and absence*

Aspen seedlings were present in 235 (31.8%) of the 739 trail segments sampled in 1996 (Table 1). Aspen seedlings only occurred in burned forest, but not all burned forest locations contained aspen. Of 631 trail segments in burned forest, aspen seedlings were absent along 396 (63%) segments. Logistic regression revealed that the presence of aspen seedlings was best predicted by the presence of burned forest and the distance to nearest adult aspen (Table 3a). Aspen seedlings were more likely to be found at distances nearer to adult aspen. Mean distance to adult aspen for the 235 segments containing aspen was 5.8 km (range was 0.1 to 14.7 km).

Presence of aspen seedlings at low ( $< 2000$  stems  $\text{ha}^{-1}$ ) and high ( $> 2000$  stems  $\text{ha}^{-1}$ ) densities was best predicted by presence and severity of burned forest, elevation, and distance to nearest adult aspen (Table 3b). Higher densities of aspen were observed in more



Table 4. Number of trail segments with aspen seedlings present and absent as predicted by the logistic regression model obtained from the 1996 data and as observed along new trails sampled in 1997. Correct predictions are in bold. Overall accuracy of the logistic model predictions was 72% [(64 + 29)/129].

Observed number of trail segments	Number of trail segments as predicted by logistic regression		
	Aspen present	Aspen absent	Row total
Aspen present	<b>64</b>	18	82
Aspen absent	18	<b>29</b>	47
Column totals	82	47	129

severely burned forest (crown fires) at lower elevations and at distances closer to mature aspen. Two additional variables were also significant. Higher densities of aspen were more likely to occur on the less fertile rhyolite substrates and in forest habitat.

When compared to the independent data set collected during 1997, the logistic model performed well (Table 4). No aspen were observed along trail segments that were unburned in 1988 and for which the probability of finding high-density aspen was very low. Overall, the model predicted 72% of all test sites correctly. Areas with and without aspen were both predicted well: 63% of non-aspen sites were predicted correctly by the model, and 78% of sites actually containing aspen seedlings were predicted correctly. Errors in predicting aspen locations were evenly balanced between errors of omission and commission, indicating a model that was not systematically biased. The  $Tau_p$  value for the model was 0.41, indicating that 41% more sites were classified correctly than would be expected by random pairing of the same number of predicted and observed aspen sites.

#### Aspen seedling density

When aspen seedlings were present along a trail segment, densities ranged over three orders of magnitude, from 31 seedlings/ha to 46,700 seedlings/ha (Table 1) with a median density of 2,000 seedlings/ha. Densities  $\geq 10,000$  seedlings/ha were observed along 52 trail segments. Thus, aspen seedlings could be very abundant locally, although they were patchily distributed across the landscape. Variation in aspen seedling density among geographic regions of the park was also apparent (Table 1). Aspen seedlings were most abundant in the south central and southwest central regions of the park, approximately an order of magnitude less abundant in the southeast region, and nearly absent in the north central area.

Table 5. Results of multiple regression analysis to explain fine-scale ( $\leq 200$  m) variation in density of aspen seedlings in trail segments in which aspen seedlings were present ( $n = 235$ ). Adjusted overall model  $r^2 = 0.31$ . See methods for description of ordinal rankings of categorical variables.

Variable	Partial $r^2$	Model $r^2$	P
Elevation	0.273	0.27	0.0001
Geologic substrate rank	0.022	0.29	0.0072
Burn severity class	0.015	0.31	0.0248
Cover type	0.01	0.32	0.0763
Topographic class	0.01	0.33	0.0924

#### Fine-scale variation

When aspen were present, 33% of the variation in aspen density at scales  $\leq 200$  m was explained by variables measured in this study (Table 5). Variation in density among trail segments was largely explained by elevation with minor explanatory power added from geologic substrate, burn severity, cover type, and topographic position. Aspen were more abundant at lower elevations ( $r = -0.52$ ,  $P = 0.0001$ ), on rhyolite substrates, in more severely burned areas, and in forest cover. Recall that aspen seedlings were only observed in burned forest, and the occurrence of burned forest was most important in explaining the presence of aspen seedlings. It is noteworthy that the distance to mature aspen was significant in explaining aspen presence/absence but not significant in explaining fine-scale variation in aspen seedling density where present.

#### Broad-scale variation

Cover type, elevation, slope, aspect and burn severity explained 72% of the broad-scale ( $> 1$  km) variation in aspen seedling density (Table 6). Seedling density increased with presence of forest habitat and was higher along trails at lower elevation and with higher burn severity. Density was greater on south-facing aspects and lower on steep slopes.

Table 6. Results of multiple regression analysis to explain broad-scale (> 1000 m) variation in aspen seedling density averaged across sampled trails (n = 18) as a function of the independent variables. Mean density included all trail segments, with and without aspen seedlings; adjusted overall model  $r^2 = 0.60$ . See methods for description of ordinal rankings of categorical variables.

Variable (sign of relationship)	Partial $r^2$	Model $r^2$	P
Cover type (+)	0.353	0.35	0.0093
Slope class (-)	0.128	0.48	0.0611
Elevation (-)	0.089	0.57	0.1428
Aspect class (+)	0.084	0.65	0.0991
Burn severity (+)	0.063	0.72	0.1281

## Discussion

### *Distribution and abundance of aspen seedlings*

Aspen seedlings varied in presence and abundance across the Yellowstone landscape. The occurrence of aspen seedlings was explained by the presence of burned forest and the distance to mature aspen stands. Once present, however, variation in seedling density was explained largely by elevation, with other factors significant but explaining a minor amount of variation.

The importance of burned forest in determining distribution of aspen seedlings concurs with previous observations that aspen seedling establishment has only occurred in burned areas (Kay 1993; Romme et al. 1997). Burned sites provide two of the three factors most critical to successful aspen germination and establishment: availability of suitable substrate and lack of competition, both of which are present following fires (the third factor is cool, moist summer weather during the year of germination). Fire consumes the accumulated litter layer, exposing mineral substrate suitable for germination and establishment of aspen seedlings. Fire also kills the trees, some ground-layer plants, and at least the aboveground portion of sprouting ground-layer species, such that both above- and belowground competition is drastically reduced for the first few years following a fire. The combination of reduced competition and a high light environment can allow aspen seedlings to grow and elongate rapidly during the initial post-fire period.

Distance to mature aspen stands was also significant in predicting the occurrence of aspen seedlings but not the density of seedlings once they were present. Aspen is wind-dispersed with small, light seeds that can travel long distances, even blowing

over snow; we observed aspen seedlings on sites that were nearly 15 km from adult aspen. Our results suggest that the proximity of suitable colonization sites to seed sources is important for aspen seedling occurrence, but that other local factors influence the local density of seedlings that establish successfully. In addition, although we observed little ramet production in excavated aspen seedlings (Romme et al., submitted), it is possible that some locations were more conducive to ramet production, which could produce higher stem densities.

The importance of elevation in explaining variation in aspen seedling density concurs with trends in the distribution of mature aspen clones throughout the northern Rockies. Aspen occupies a wide elevational range overall, but adult clones are most prevalent at elevations of 1830–2290 m (Mueggler and Campbell 1982). The upper end of this distributional range coincides with the lower end of the elevational range encompassed by our study. Although Romme et al. (1997) found no effect of elevation on broad-scale seedling distribution, that study had fewer observations and spanned a more narrow range of elevation. These new results suggest that recruitment of new aspen stands may be most likely at elevations < 2300 m. At higher elevations, lower temperatures or increased snow accumulation may limit aspen growth and survival. For example, we have observed overwinter dieback of the prior year's growth on unburned aspen seedlings occurring at high elevations (personal observations).

Several other variables were significant but explained a small proportion of the variance in aspen seedling density. Aspect and slope were significant in the broad-scale analyses, and these are most likely surrogates for complex variation in moisture availability across the landscape. Shallower slopes, which had greater aspen seedling densities, tend to collect and retain more moisture for longer periods than steeper slopes. Gentle slopes may also be more likely to capture and retain aspen seeds than steep slopes. Southerly aspects have greater exposure to solar radiation and are generally drier than northerly aspects, but at higher elevations snow melt on southern slopes may coincide better with the timing of spring seed set in aspen, such that aspen seeds may germinate and seedlings establish better on exposed, moist southern slopes than on snow-covered northern slopes. Given the location of our study sites near the upper elevational limit of aspen, where low temperatures and short growing seasons may be important factors lim-

iting aspen survival, the more moderate climate of south-facing slopes may be especially important. Southerly slopes, exposed to the prevailing southwesterly wind, may also collect seed better than northerly slopes. Combinations of slope, aspect, elevation, and local topographic features that provide the required moisture conditions will facilitate the establishment of aspen seedlings.

We also observed that aspen seedling densities were conspicuously high in some geographic regions of the park (e.g., southwest central area) and apparently absent in others (e.g., north central area). This regional pattern may result, in part, from very broad-scale topography. The occurrence of the highest densities of aspen in the southwest central region is partially attributable to the moderate elevations, presence of large areas of contiguous burned forest in this area, and the numerous small patches of shrubby adult aspen in rocky outcrops along the major river valleys. In addition, the southwest central region is located just northeast of a major concentration of adult aspen clones in the Bechler region of YNP and Targee National Forest. This landscape position places it directly in the path of the prevailing southwest winds, with no substantial topographic barriers downwind to block seed dispersal from these more distant populations. In contrast, the occurrence of low aspen seedling densities in the southeast region, where there are also large, contiguous areas of burned forest, may be explained by its high elevation, paucity of local adult aspen clones, and the presence of high mountains that may inhibit seed dispersal from more distant populations. The extremely low densities of aspen seedlings in burned forests in the north central portion of YNP may be due to inadequate seed dispersal from adult aspen clones. Local patches of adult aspen are rare or absent in this area. The nearest adult aspen clones are in northern YNP, but they are located downwind from the subalpine plateau and  $\sim 500$  m lower in elevation. Genetic analyses by Tuskan et al. (1996) indicated that none of the post-fire seedling populations sampled on the subalpine plateau were direct progeny of mature aspen stands in northern YNP.

Our results ( $r^2$  values) also suggest that there are other significant components of environmental variation that influence aspen seedling density that our measured set of variables did not include. Such factors could be biotic (e.g., lodgepole pine seedling density, cover of herbaceous vegetation, or herbivory) or abiotic (e.g., precipitation, depth of snow pack, landscape-scale topographic position, or duration of

spring moisture). Genetic diversity within aspen seedling populations in Yellowstone is negatively related to percent cover of herbaceous vegetation (Stevens et al. 1999), suggesting that competition-induced mortality of seedlings may be underway.

#### *Aspen seedlings – aspen stands? Landscape-scale implications*

Large, infrequent disturbances, such as the Yellowstone fires of 1988, provide important opportunities to examine and understand landscape dynamics influential for variations in the ranges of plant populations. For quaking aspen, the infrequent occurrence of extensive fires in the northern Rocky Mountains may afford the potential for significant range expansion of this species. The frequency and extent of fires in YNP is likely to increase if the climate becomes warmer and drier (Balling et al. 1992), and both the upper and lower elevational limits for species may change (Romme and Turner 1991; Bartlein et al. 1997). More frequent fires would result in the increased occurrence of bare mineral substrates and competition-free colonization sites necessary for successful aspen regeneration.

Other factors, however, may interact to prevent aspen from expanding its range. A warmer, drier climate might also increase drought, reducing the suitability of conditions for aspen seedling establishment and growth. Moreover, successful aspen establishment apparently did not occur following large fires on the Yellowstone Plateau in 1910, 1931, 1946, and 1981, either because of inadequate seed dispersal and germination, or high mortality rates among seedlings. We say this because we never saw aspen in the areas burned by these earlier fires during extensive field work from 1977 to 1987 (Romme and Despain 1989). Thus, the persistence time of the aspen seedlings documented in this study remains unknown.

Browsing by ungulates has been implicated as a key proximate factor preventing recruitment of tree-sized individuals from both seedling and sprouting aspen (e.g., Romme et al. (1995) and Baker et al. (1997), Kay and Bartos (2000)). Aspen is a preferred browse of elk and moose (Jones 1974; DeByle 1985a; Boyce 1989), and large ungulates often graze preferentially in recently burned areas (Hobbs and Spowart 1984; Boyce and Merrill 1991; Pearson et al. 1995) because of the abundance of highly nutritious herbaceous vegetation. Thus, aspen seedlings in burned forests may be exposed to high levels of ungulate brows-

ing which could prevent aspen seedlings from persisting to adulthood as a significant component of the post-fire vegetation mosaic. Browsing rates have been as high as 80–100% of aspen seedlings in some years (M. G. Turner and W. H. Romme, unpublished data), and this high intensity of herbivory may preclude establishment of new aspen clones. Aspen seedlings produce secondary defense compounds (Erwin et al. 2001), but these may not be effective deterrents to elk herbivory. The combination of ungulate browsing, which maintains low-stature aspen plants, and competition from rapidly growing post-1988 lodgepole pine saplings may prevent most aspen seedlings from achieving tree stature. However, the substantial amounts of coarse woody debris produced as the fire-killed trees have fallen may reduce elk herbivory (Ripple and Larsen 2001). In at least two locations in the west-central portion of YNP, where meter-deep piles of fallen pine boles discourage ungulate browsing and the low elevation provides a relatively long growing season, many aspen seedlings that established in 1989 were 1–2 m tall in 2001 (personal observations). Thus, new aspen clones may develop only in sites with abundant coarse woody debris, favorable microclimate and relatively sparse densities of lodgepole pine saplings.

The ultimate question regarding recent aspen seedling recruitment across the subalpine plateau is whether these seedlings represent merely an interesting, but passing, aspect of post-fire successional dynamics, or whether the seedling populations will achieve tree stature, produce ramets, and develop into adult aspen stands. If these seedlings give rise to new adult aspen stands across the plateau, it would represent a fundamental change on the Yellowstone landscape. Extensive areas of aspen forest in a landscape previously dominated by coniferous forest would have significant implications for landscape diversity, spatial vegetation patterns, future successional dynamics, species habitat use and migratory patterns, and a multitude of ecosystem processes (e.g., biogeochemical cycles). Understanding the factors influencing potential future patterns or species across the landscape is critical for understanding and managing our natural and managed landscapes.

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