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RESEARCH ARTICLE

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Population Condition of *Populus × smithii*, a Pleistocene Relict Aspen of the Niobrara River Valley, Nebraska, USA

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ABSTRACT: At Smith Falls State Park in northern Nebraska, a relict population of *Populus* × *smithii*, a hybrid of quaking aspen (*P. tremuloides*) and bigtooth aspen (*P. grandidentata*), has been targeted for management due to its rarity and risk of extirpation. This relict occurs under favorable microclimatic conditions in springbranch canyons along the Niobrara National Scenic River, but factors such as climate change, lack of regeneration, and competition with invasive juniper (*Juniperus virginiana*) make its persistence tenuous. This study was designed to assess the overall health of the Smith Falls aspen population and determine whether individual stands ($n = 10$) differed in condition, whether these differences in condition were related to environmental or demographic variables, and whether the condition of the stands was worsening. We found evidence of a declining aspen population, with crown loss and limb dieback documented across all size classes and worsening over a period of two y. Trees from younger, smaller size classes displayed less damage than older, larger ones, but accrued more damage over the two-y interval. At the stand level, higher levels of damage occurred in stands with larger area, more individual boles, and larger, older trees. Our findings suggest that this unique relict population of aspen is showing significant signs of decline but has potential to survive if managed with ecological principles of succession in mind.

Index terms: aspen decline, Great Plains, population structure, *Populus* × *smithii*, relict population

INTRODUCTION

In the Great Plains of the central United States, quaking aspen (*Populus tremuloides* Michx.) is sparsely distributed among bluffs, escarpments, and river valleys. More common in northern and montane regions, the wide distribution of this species was shaped by the last glacial maximum, a period of rapid climate change wherein boreal forests were pushed to more southerly regions (Kaul et al. 1988; Callahan et al. 2013). In Nebraska, steep canyons and draws watered by springs and seeps provide refuge from the now semi-arid climate for aspen and other Pleistocene relicts found only in the Pine Ridge escarpment and the Niobrara River Valley (NRV) (Tolstead 1942; Kaul et al. 1988). The NRV constitutes a riparian corridor with a unique assemblage of trees from both eastern and western North America, with many species at the limits of their native ranges (Kaul et al. 1988). Among them is a rare hybrid aspen, *Populus* × *smithii* B. Boivin (*grandidentata* × *tremuloides*), found at Smith Falls State Park and adjacent properties (Figure 1). Parental *P. tremuloides* can still be found nearby at the Valentine National Wildlife Refuge, but the nearest documented occurrence of the other parent species, bigtooth aspen (*Populus grandidentata* Michx.), is some 350 km east in central Iowa (Barnes 1961).

Recent nuclear microsatellite and chloroplast sequence analysis of this population and its nearest parent species has confirmed it as a hybrid of *P. tremuloides* and *P. grandidentata* (Deacon et al. 2017). Although other stands of *P.* × *smithii* are found in the northeastern United States and Great Lakes regions, this population's extremely disjunct placement and marginal habitat make it a target for conservation (Eckenwalder 2010) and it is considered "critically imperiled" in the state of Nebraska (NatureServe 2017). North American aspen stands have exhibited recent widespread decline, with dieback and stand death documented in western North America (Frey et al. 2004; Hogg et al. 2008; Anderegg et al. 2011). Research suggests that aspen decline is primarily occurring in places that are at the edge of aspen's climate envelope, wherein potential evapotranspiration exceeds annual precipitation (Hogg 1994, 1997). Climate models generally project increases in temperature and modest increases in precipitation for the northern Great Plains (Allen et al. 2010; IPCC 2007a, 2007b), and the lower elevation limit at which climate supports aspen is expected to increase by 750 m by the end of the century (Sturrock et al. 2011).

Forest decline has already been documented in the NRV in another relict boreal species, paper birch (*Betula papyrifera* Marshall). Stroh and Miller (2009) examined climate data from 1948 to 2007 for the NRV and found that more variable springtime temperatures over the last 30 y could threaten the protective microclimates of the NRV refugia. These conditions could lead to rootlet damage in paper birch and

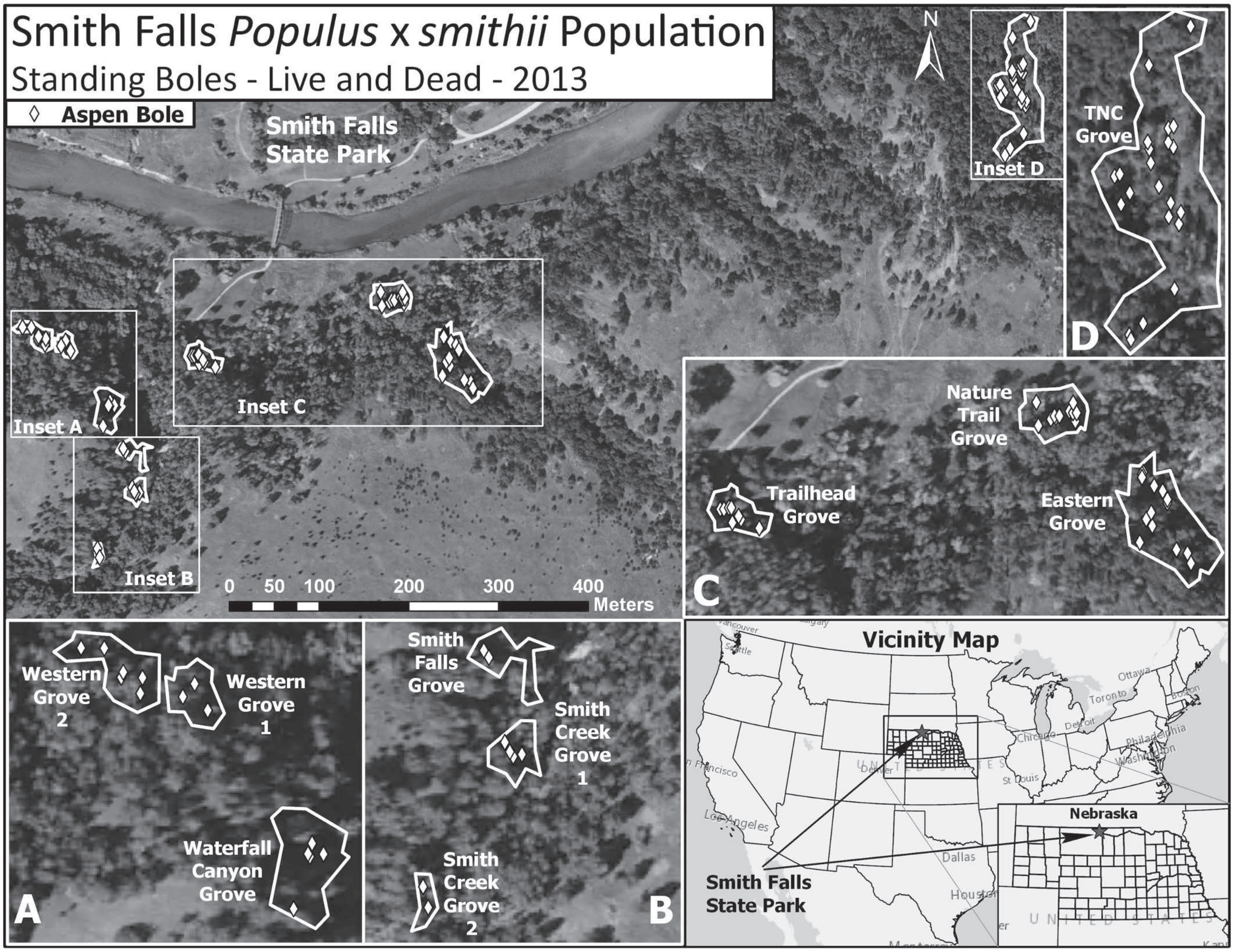

Figure 1. The mature aspen trees examined in the NRV for this study are distributed in 10 separate stands along the southern side of the Niobrara River in Smith Falls State Park and the Niobrara Valley Preserve (TNC).

are likely associated with recent crown dieback events and lack of regeneration (Stroh 2011). While aspen can withstand moderate water deficits, severe drought stress impairs stomatal and root-water conductivity (Siemens and Zwiazek 2003) and is suspected to be at the core of landscape-level aspen decline, which can occur rapidly (Worrall et al. 2010; Sturrock et al. 2011). This is of particular concern for the relict hybrid aspen stands occurring in microclimatic refugia in the NRV, where climate change has the potential to trigger widespread tree mortality (Stroh and Miller 2009; Stroh 2011; Anderegg et al. 2013). Topographic position could influence water availability and tree drought stress within the microclimatic refugia where the aspen occurs (Evans 2010). Clonal reproduction in aspen occurs via suckering rootlets (White et al. 1998; Namroud et al. 2005) making their regeneration physiologically susceptible to the variable climate patterns documented for the NRV (Siemans and Zwiezak 2003; Stroh 2011).

This study was designed to examine the status of this relict aspen population because its stands are small and disjunct, and hence susceptible to extirpation (Woodward 1987). Our objectives were to (1) assess the current health of the aspen stands at Smith Falls State Park in the NRV and determine if there is evidence of significant aspen decline; (2) determine whether topographic position and demographic conditions such as size structure and stand area reflect variations in tree and population health among stands; and, to inform management, (3) identify the stands that are most at risk of extirpation. We hypothesized that the age structure of this population would be weighted toward older individuals due to a changing climate profile and a lack of disturbance at the site, and that stands with a younger composition would be the healthiest and bear the fewest signs of decline.

METHODS

Aspens are found growing patchily along the NRV downstream of Valentine, in Cherry County, Nebraska (Kaul et al. 2010). The *P.* × *smithii* population in the NRV exists in 12 small stands found solely south of the river on the floodplain and north-facing slopes from 670- to 750-m elevation (Figure 1; Table 1). These include 10 stands at Smith Falls State Park, another upstream on private land used for cattle grazing, and one more downstream in The Nature Conservancy's (TNC) Niobrara Valley Preserve.

Modern management of *P.* × *smithii* in the NRV began in 1991, when the U.S. Congress designated the 122-km stretch of the Niobrara east of Valentine as a National Scenic River (Davenport and Anderson 2005) because of its primitive watershed, largely undeveloped shoreline, and outstanding cultural, recreational, and biological value (www.nps.gov/niob). Following this action, the Nebraska Game and Parks Commission worked in tandem with the Krzyzanowski family (landowners) to establish Smith Falls State Park in 1992, with the intention of maintaining the area in a natural state, providing access to visitors while protecting sensitive biota, particularly the aspen. Heavy foot traffic and cattle grazing over the previous decades had caused significant erosion and threatened the natural status of the area.

The next significant management step involved the systematic clearing of eastern red cedar (*Juniperus virginiana* L.) from aspen stands at Smith Falls State Park between 2009 and 2012. Following the establishment of fire suppression practices in the eastern Great Plains, red cedar has become abundant to the point of excluding other species due to its thick canopy (Gehring and Bragg 1992; Frost and Powell 2011). Clearing of red cedar from aspen stands is known to spur an increase in suckering (Brinkman and Roe 1975; Prevost and Pothier 2003) and efforts at the Park were coupled with those of private advocacy groups like the Western Nebraska Resources Council in the adjacent Niobrara Valley Preserve (TNC Niobrara Valley Preserve 1999).

Table 1. Summary statistics for 10 stands of mature aspen (*Populus* × *smithii*) at Smith Falls State Park and the Niobrara Valley Preserve (TNC) in the Niobrara River Valley (NRV) of northern Nebraska based on sampling in 2013 and 2015. Data are presented from smallest to largest stand, according to the number of boles in the stand.

Stand name	Stand area (ha)	dbh (cm) mean (SD)	# trees 2013	# live trees 2013	% live trees 2013	# trees 2015	# live trees 2015	% live trees 2015	Mean (SD) damage score 2013	Mean (SD) damage score 2015	Mean (SD) % crown death 2013	Mean (SD) % crown death 2015
Smith Creek Grove 2	0.04	17.3 (0.2)	2	2	100	2	2	100	2.5 (-0.7)	2.00 (1.41)	7.5 (10.6)	5 (-7.1)
Smith Falls Grove	0.13	27.3 (6.8)	3	2	67	3	2	67	5 (-2)	5.33 (1.53)	63.3 (35.1)	56.7 (40.4)
Western Grove 1	0.22	24.1 (7.2)	3	3	100	3	3	100	4 (-1)	4.33 (1.15)	40 (-15)	55 (39.7)
Smith Falls Creek Grove 1	0.17	19.5 (8.5)	4	3	75	3	2	67	4.25 (2.5)	4.67 (2.08)	56.25 (40.9)	51.7 (42.5)
Waterfall Canyon Grove	0.28	26.4 (7.3)	5	3	60	5	2	40	5.00 (2.35)	5.80 (1.79)	65 (42.9)	79 (39.1)
Western Grove 2	0.18	21.6 (6.8)	6	5	83	5	4	80	4.83 (1.47)	4.40 (1.67)	53.3 (34.9)	38 (38.2)
Trailhead Grove	0.25	16.0 (8.2)	10	9	90	10	7	70	3.90 (1.73)	4.50 (2.01)	39.5 (31.8)	49.5 (42.4)
Nature Trail Grove	0.58	20.1 (15.1)	13	7	54	9	6	67	5.00 (2.24)	4.44 (1.94)	60.8 (44.8)	48.9 (39.2)
Eastern Grove	1.05	41.3 (6.2)	14	8	57	13	7	54	5.43 (1.50)	5.54 (1.45)	65.7 (32.7)	72.7 (30.4)
Nature Conservancy Grove	1.1	28.9 (8.0)	20	12	60	16	9	56	5.15 (1.84)	5.25 (1.73)	65.8 (36.0)	60 (40.1)
Means (SD)	**0.4 (0.4)**	**24.25 (7.00)**	**8 (5.7)**	**5.4 (3.3)**	**74.6 (16.8)**	**6.9 (4.6)**	**4.4 (2.4)**	**70.0 (18.1)**	**4.51 (0.83)**	**4.63 (1.01)**	**51.72 (17.47)**	**51.64 (19.16)**

Sampling Design

Although there are 12 separate *P.* × *smithii* stands present in Smith Falls State Park and the adjacent properties (TNC, private) in the NRV region, only 10 stands were included in data collection and analysis (Table 1; Figure 1). One stand (on private land) was excluded as it was heavily weighted toward older individuals due to ongoing cattle grazing, and the other (in Smith Falls State Park) because it lacked any standing mature trees. Due to potential stresses that could be caused by coring, the size structure of standing trees was used as a surrogate for age classes, assessed in four bole dbh categories: 5–15 cm, 15–25 cm, 25–35 cm, and >35 cm (adapted from Worrall et al. 2010). Mature trees were deemed those over 5-cm dbh, and smaller ones deemed saplings. Sapling condition and density were measured along transects within a subset of the aspen stands, with results reported in a related paper (Robertson et al. 2018).

During the summer of 2013, all individual standing ramets of *P.* × *smithii* ($N = 80$) that were ≥5 cm dbh, both live and dead, were measured within the nine stands in Smith Falls State Park and one in the adjacent TNC Niobrara Valley Preserve (Table 1). Dead boles were included as they may have been alive in recent years and may represent an active root network that could be significant for sucker formation. Circumference at breast height was measured and used to calculate dbh. The presence of pests, pathogens, and damage was noted, and the percentage of crown death was visually estimated. The location of each tree was mapped to within 5 m using a Garmin GPS unit. The trees were relocated and resurveyed for damage in August 2015 ($N = 69$) to determine whether stand condition had significantly deteriorated during that 2-y period. The population was lower in 2015 because 10 dead boles and 1 live bole had fallen during the intervening 2 y.

Damage Scale

We created a damage score based on the severity of crown dieback to assess the health of each sampled tree. This score used a seven-stage scale, based on the damage scale used by Stroh and Miller (2009) in their study of paper birch in the NRV:

1. Normal, apparently healthy tree;
2. Trees with abnormally small, thin, curled, chlorotic foliage (any one or combination);
3. Trees with bare or dead twigs, but with no dead branches;
4. Trees with dead branches constituting <50% of the crown;
5. Trees with >50% of the crown dead;
6. Foliage only on one to several trunk sprouts;
7. Tree entirely dead.

Individual aspen trees were grouped into their constituent stands, and the total number of boles, percent living aspen, and other tree species in the immediate area were recorded. Stand areas were provided by the National Park Service and used to determine aspen stem density in each stand.

Statistical Analysis

Given the ordinal (damage scale) or otherwise non-Gaussian (percent crown death) distribution of much of our data, we used nonparametric analyses for most statistical comparisons. Kruskal-Wallis tests were used to analyze differences in median damage scores and percent crown death among the four size classes of boles across stands in 2013 and 2015, with post hoc comparisons using pairwise Kruskal-Wallis tests with a sequential Bonferroni procedure to control experiment-wise error to $\alpha \leq 0.10$. Damage scores and percent crown death were also analyzed between two lumped size classes of smaller (<25 cm dbh) and larger (>25 cm dbh) trees using Kruskal-Wallis tests. Spearman's rank correlations were used to test for associations between measures of stand-level damage (mean damage score, % mean crown death, and % living trees per stand) and stand characteristics (stand area, tree density, number of trees per stand, and mean dbh). Kruskal-Wallis tests were used to compare median % crown death and damage score for trees in floodplain (695–700-m elevation) and ridge (700–745 m) topographic positions. Wilcoxon signed rank tests and paired *t*-tests were used to test for changes in health metrics of individual trees from 2013 to 2015.

RESULTS

Size Class Predicts Health Status

While most stages of the damage scale occurred in all size classes of aspen, there were notable exceptions (Figure 2). In the 2013 sample, only the smallest size class of mature aspen trees (5–15-cm dbh) included boles with no evident damage (stage 1, healthy) and, across the population, only in this size class were all of the damage stages present. This size class featured the healthiest individuals, with 40% (8 of 20) assessed as healthy or showing only light damage (stages 1–3) in 2013 and 50% (9 of 18) in 2015. In the 2015 sample, however, only two boles total (one in the 5–15- and one in the 15–25-cm dbh class) showed no evident damage across the entire population. Among aspens in the largest size class (dbh > 35 cm), higher levels of damage were ubiquitous, with 96% (22 of 23) showing dead branches and partial or total crown death (stages 4–7; Figure 2) in 2013 and 100% (all 21 standing stems) showing these levels of damage in 2015. Considering all of the aspen, intense damage stages (4–7) were observed in 73.5% of all trees (59 of 80) in 2013 and 68.1% (47 of the 69 standing boles) in 2015. For trees >25-cm dbh, nearly all (90.5% in 2013, 91.2% in 2015) had dead branches or significant crown dieback. Overall, 17 of the 42 trees (40%) in 2013 and 14 of 34 (41%) in 2015 in the large size classes (>25-cm dbh) were dead, whereas only 9 of the 38 (24%) smaller trees (<25-cm dbh) were dead in 2013 and 11 of 35 (31.4%) in 2015. Overall, 32.5% (26 of 80) of the total population of standing boles was composed of dead trees in 2013 and 36.2% (25 of 69) in 2015. The difference in sample size between the two years reflects the loss of 11 boles (1 living, 10 dead) that fell between 2013 and 2015.

There were significant differences in damage among aspen size classes (Kruskal-Wallis, $\chi^2 = 8.6903$, df = 3, $P = 0.0337$) in 2013, with damage scores significantly lower for aspen in the 15–25-cm dbh class

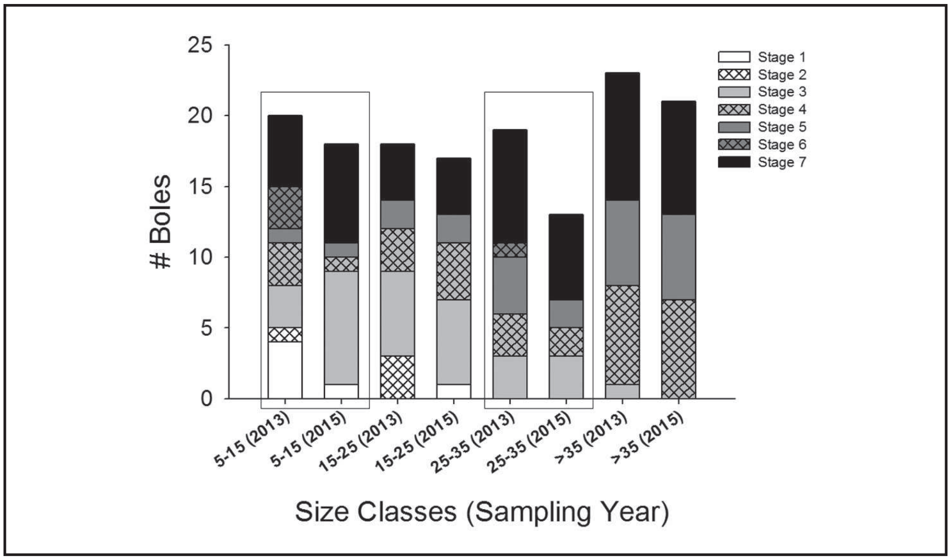

Figure 2. Damage levels across four size classes (cm dbh) of aspen boles sampled in 2013 and 2015. Totals differ between years because fallen trees were not resampled. Damage stages are as follows: 1. Healthy, no damaged limbs; 2. Abnormally small curled chlorotic foliage; 3. Bare or dead twigs; 4. Dead branches (<½ crown); 5. >½ crown dead; 6. Trunk sprouts only; 7. Dead.

than in the >35-cm dbh class (Kruskal-Wallis, $\chi^2 = 6.5468$, df = 1, $P = 0.0105$). Differences in median damage scores between the 15–25 cm and 25–35-cm size classes were nearly significant (lower scores for 15–25 cm, Kruskal-Wallis, $\chi^2 = 5.1462$, df = 1, $P = 0.0233$) when compared to sequential Bonferroni-adjusted α values. The 5–15-cm size class, with its wide range of damage scores, did not differ significantly from any other size class. Overall patterns were similar, but weaker, in 2015, with no significant differences in damage scores among size classes (Kruskal-Wallis, $\chi^2 = 6.0301$, df = 3, $P = 0.1102$). When aspen dbh values are reclassified into just two size classes, however, the largest (>25-cm dbh) aspen showed significantly more damage than the smallest (<25-cm dbh) in both 2013 (Kruskal-Wallis, $\chi^2 = 8.4558$, df = 1, $P = 0.0036$) and 2015 ($\chi^2 = 5.7097$, df = 1, $P = 0.0169$).

Percentage crown dieback also varied significantly among the four dbh size classes (Kruskal-Wallis, $\chi^2 = 9.2620$, df = 3, $P = 0.0260$) in 2013, with lower values in the 15–25-cm class than in the 25–35-cm (Kruskal-Wallis, $\chi^2 = 6.2816$, df = 1, $P = 0.0122$) and >35-cm ($\chi^2 = 6.8017$, df = 1, $P = 0.0091$) classes. In 2015, differences in percent crown dieback values were weakly significant (Kruskal-Wallis, $\chi^2 = 7.5699$, df = 3, $P = 0.0583$), with significantly lower values in the 15–25-cm class than the >35-cm class ($\chi^2 = 7.1487$, df = 1, $P = 0.0075$). For dbh values reclassified into just two classes, aspen with dbh > 25 cm had significantly greater percentage crown dieback than those <25 cm in both 2013 (Kruskal-Wallis, $\chi^2 = 8.6589$, df = 1, $P = 0.0033$) and 2015 ($\chi^2 = 5.5914$, df = 1, $P = 0.0180$).

At the stand level, mean aspen dbh was strongly positively correlated with mean damage score ($r_s = 0.865$, $P = 0.0012$) and mean percentage crown death ($r_s = 0.855$, $P = 0.0016$), and weakly negatively correlated with % of living boles in the stand in 2013 ($r_s = -0.555$, $P = 0.0959$; Figure 3A). Patterns were similar in 2015 (Table 2), with mean dbh positively correlated with mean damage score ($r_s = 0.636$, $P = 0.0479$) and mean percentage crown death ($r_s = 0.782$, $P = 0.0075$) and negatively related to % of living boles ($r_s = -0.622$, $P = 0.0550$). These correlations for 2015 were based on the 2013 dbh measurements, as dbh was not remeasured in 2015.

Changes in Stand Health from 2013 to 2015

When we resurveyed the aspen stands in 2015, we saw evidence of a general decline in stand health and abundance among *P.* × *smithii* (Figure 2). What started as a population with 54 living (80 total standing boles) trees in 2013 was reduced to 44 (69 standing boles) in 2015; nine of the living trees from 2013 died and remained standing while one previously living tree died and fell. This was a stark change for the population, constituting an 18.5% loss of the living mature trees over a 2-y period. For trees that were alive in 2013 and still standing in 2015 ($N = 53$), there was a significant increase in damage score (0.51 on average; paired *t*-test: $t_{52} = 3.42$, $P = 0.0012$; Wilcoxon signed rank: $S = 148$, $P = 0.0007$) and percentage dead crown (6.7% increase on average; $t_{52} = 2.23$, $P = 0.0304$; $S = 161.5$, $P = 0.0340$) from 2013 to 2015. The youngest size class appeared to show the greatest declines in health: trees in the 5–15-cm dbh class showed an average increase in damage score of 0.8 ($t_{13} = 2.347$, $P = 0.0342$; $S = 20.5$, $P = 0.0430$) and an average increase in percent crown death of 8.3% ($t_{13} = 1.902$, $P = 0.078$; $S = 18$, $P = 0.0625$), with several of the trees advancing into the next damage class by developing dead branches and four of them dying (two boles that were dead in 2013 also fell).

Effects of Topographic Position

We compared condition of trees in the Niobrara River floodplain (695–700-m elevation, $N = 29$ trees in 2013, $N = 22$ in 2015) and those found in the bluffs above the river (700–745-m elevation, $N = 51$ trees in 2013, $N = 47$ in 2015). There were no significant differences in median damage score (Kruskal-Wallis: $\chi^2 = 0.736$, df = 1, $P = 0.391$ for 2013; $\chi^2 = 0.211$, df = 1, $P = 0.654$ for 2015) or percent crown death ($\chi^2 = 0.456$, df = 1, $P = 0.499$ for 2013; $\chi^2 = 0.001$, df = 1, $P = 0.974$ for 2015) between populations of aspen growing in these two elevation ranges in 2013 and 2015.

Effects of Population Composition

In 2013, aspen stands with more individual boles tended to have greater mean damage scores ($r_s = 0.671$, $P = 0.0337$; Figure 4A), greater mean % crown death ($r_s = 0.614$, $P = 0.0590$; Figure 4B), and a lower percentage of living trees ($r_s = -0.688$,

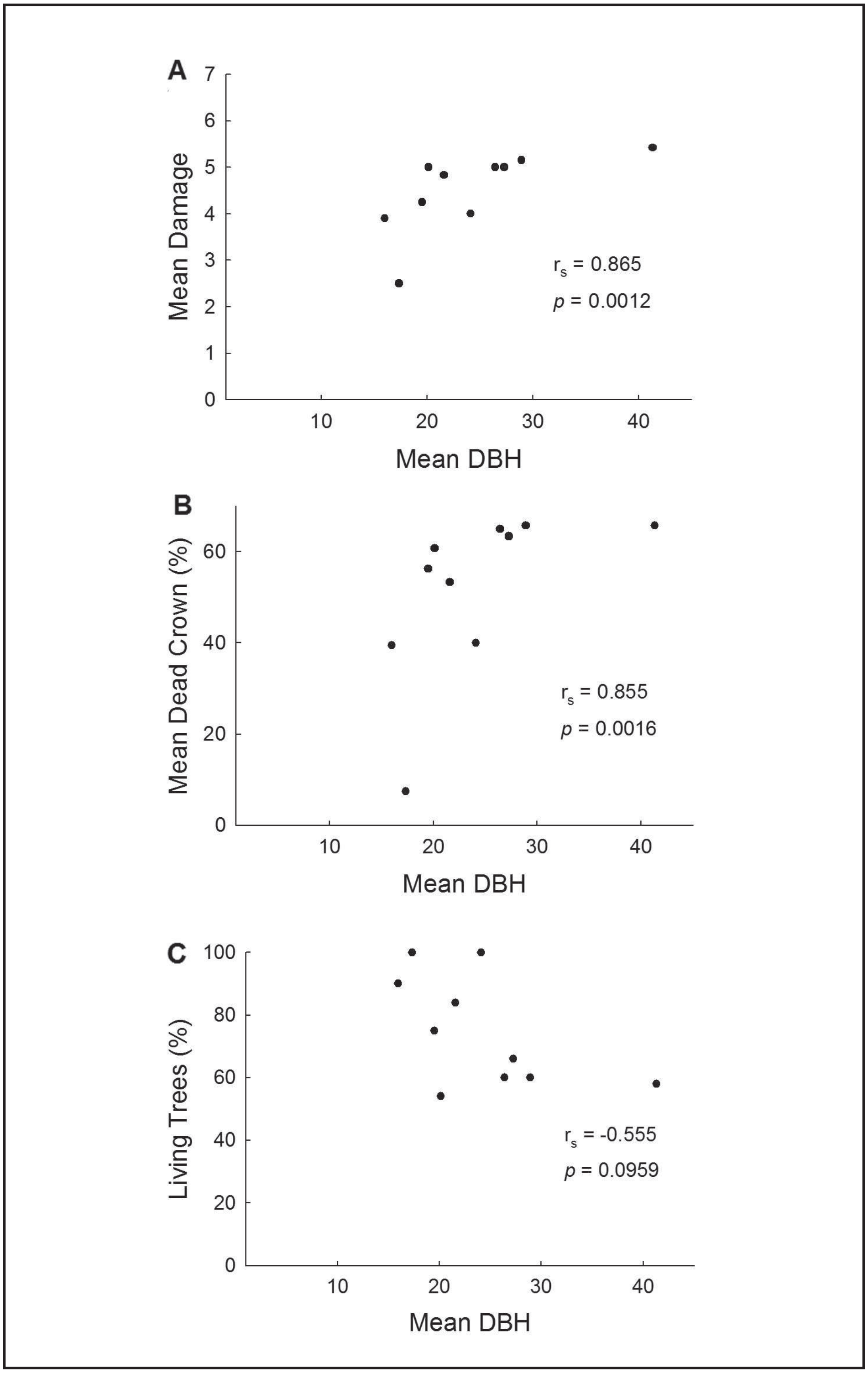

Figure 3. ***P.* × *smithii* stands in 2013 with larger average dbh (cm) tend to display greater damage as measured by (A) damage scale and (B) percent crown death. (C) Greater mean dbh was negatively associated with % living trees in the stand.**

P = 0.0278; Figure 4C). Damage scores were similarly correlated with stand area (higher damage scores, higher % crown death, and lower % living trees in stands with larger area; Table 2), which was itself strongly positively correlated with the number of boles in the stand (r_s = 0.900, P = 0.0004). Conversely, aspen stands with a greater density of boles (stems/hectare) were associated with better health metrics (lower damage score: r_s = −0.693, P = 0.0262; Figure 5A; lower percent crown death: r_s = −0.685, P = 0.0289; Figure 5B) in 2013. This may be because stand area (and number of boles) was inversely related to stand density (i.e., smaller stands had higher stem density, r_s = −0.648, P = 0.0425). Relationships were similar (same direction), but generally weaker (smaller correlation coefficient and higher P-value) in 2015 (Table 2).

DISCUSSION

Using numerous variables and multiple metrics to assess the health and viability of NRV aspen (*Populus* × *smithii*), we determined that there are two primary factors that are indicative of declining health of individual aspen and their stands in this population: the size of trees (stem diameter at breast height) and population variables like the number of trees in the stand and their density. We found that smaller individual trees as well as aspen stands with smaller mean dbh exhibited less damage and had a greater percentage of living trees per stand, but also found that the smallest dbh aspen appeared to accumulate the most damage between our 2013 and 2015 samples. Our data also showed that aspen growing in larger stands, with more individual boles, displayed increased damage metrics. Generally, younger aspen in smaller, denser stands had the least damage, whereas the older, larger, more open stands were less healthy and featured considerable crown dieback.

Topographic position relative to the floodplain had no apparent effect on tree health. This was surprising as availability of water is a limiting factor governing aspen distribution (Hogg 1994, 1997). However, the abundance of springbranch creeks along the south side of the valley means that the Smith Falls aspens, even at higher elevations, are still close to a water source (Kaul et al. 1988). The tolerance of aspen to intermittent aridity and varied soil types may make it so that any effect of elevation on this level (695–745 m, a 50-m distinction) is insignificant. The microclimate that sustains these relict trees in the canyons of Smith Falls is undoubtedly influenced more by topographic features such as slope

Table 2. Spearman's rank correlations (r_s) between stand characteristics and aspen condition metrics for 2013 and 2015 sampling ($n = 10$ stands). $P < 0.10$*, $P < 0.05$, $P < 0.01$***.**

Variables	Mean dbh	# trees/stand	Stand area	Tree density
2013				
Mean Damage Score	0.865***	0.671**	0.693**	−0.693**
Mean % crown dead	0.855***	0.614*	0.673**	−0.685**
% living trees	−0.555*	−0.688**	−0.683**	0.524
2015				
Mean Damage Score	0.636**	0.455	0.455	−0.333
Mean % crown dead	0.782***	0.400	0.539	−0.600*
% living trees	−0.622*	−0.575*	−0.634**	0.437

and aspect (e.g., all aspen stands occur on the north-facing slopes on the south side of the river) than by elevation (Stroh and Miller 2009).

Long-term factors like stand or site conditions predispose populations to acute stresses from short-term environmental or biological stressors, which can combine to lead to sudden decline, and possibly result in widespread mortality (Manion 1991; Worrall et al. 2010). Rapid declines documented in quaking aspen populations of western North America are linked to climate-related stressors compounding problems already present in the populations (Worrall et al. 2008; Rehfeldt et al. 2009). In Colorado, studies of widespread aspen decline have linked root condition to overstory health (Worrall et al. 2010) and found areas of high stand damage to be associated with greater moisture deficits during drought stress (Sturrock et al. 2011). Rehfeldt (2009) predicted a drastic reduction in areas that could support aspen's unique climate profile in the American West and showed that areas exhibiting Sudden Aspen Decline (SAD) were largely in line with predictions of loss of aspen due to climate change. Climate change could reduce the protective effect of microclimate in the springbranch canyons and endanger the aspen, putting them at risk of extirpation due to a suite of environmental, physiological, and demographic factors. An unfortunate sequence of events, even over a discrete period, that included a general increase in temperature and sudden reduction in precipitation, variable springtime freeze–thaw cycles leading to rootlet death (as with the local birch population; Stroh and Miller 2009), and chronic lack of regeneration (Robertson et al. 2018) could spell the end of the NRV aspen. Our 2015 resurvey indicates that widespread and rapid mortality may be a concern for some of the stands. In two y nearly 20% of live trees were lost, including many of those in both the youngest (dbh: 5–15 cm) and mature (dbh: 25–35 cm) size classes.

Aspen stands in the NRV bear many signs of long-term deterioration, which may dispose them to continued decline if action is not taken to alleviate stressors affecting them (Worrall et al. 2008; Sturrock et al. 2011). Our findings are consistent with recent research on aspen decline in Colorado (Worrall et al. 2010), where crown death was used as a metric for determining healthy (10.9% crown loss) and damaged (53.9% crown loss) stands. Of the ten stands at Smith Falls, seven featured mean crown loss greater than 50% (of those, mean crown death was 61.4%). Only one stand, with two trees, had crown loss less than 10%. Even when standing boles with complete crown loss were excluded from our data set, mean crown loss was still above 36%, indicating an unhealthy population. Worrall found that nearly all trees with over 70% crown loss were dead within two y, so there is cause for concern given the worsening condition of heavily damaged trees in the NRV and the observed die-off between 2013 and 2015.

Our observations show numerous symptoms of aspen forest decline present in these stands; the most pronounced being synchronous dieback of branches and a lack of regeneration among smaller size classes (Worrall et al. 2008; Robertson et al. 2018). Substantial crown dieback was displayed across all sizes of aspen, with significantly more occurring in larger trees. The smaller size classes (5–15 and 15–25 cm) included many dead and heavily damaged boles (categories 4–7) and were heavily damaged over a 2-y period. Senescence of older, mature trees has not resulted in increased recruitment of young-mature trees in the smaller size classes in the absence of disturbance, shown by the relatively even distribution of individuals among size classes (Figure 2). Damage and mortality among the larger size classes (25–35 and >35 cm) is not in itself alarming in this short-lived early successional species, as older trees have more time to accrue the physiological signs of stress. On the other hand, high and rising damage levels and dieback of smaller trees point to other stressors in the ecosystem, in addition to lack of disturbance.

Competition from invasive red cedar—only recently cleared from the stands—likely inhibited understory light penetration as aspen in these smaller size classes were beginning to grow (Ares et al. 2010). Browsing by ungulates in the absence of natural predators has been shown to significantly inhibit clonal recruitment and expansion in aspen (Ripple et al. 2001; Edenius and Ericsson, 2007; Forester et al. 2007), and the NRV includes a healthy population of white-tailed deer (*Odocoileus virginianus* Zimmerman). Abundant suckering has occurred in many stands following the removal of red cedar, but heavy browsing by deer has largely restricted sapling growth and survival to deer exclosures and brush piles that prevent deer access (Robertson et al. 2018). Even the presence of parasitic pests, such as oystershell scale and cytospora cankers, which were seen on many of the young trees, may play a role in inhibiting their growth and hastening mortality (Hogg et al. 2002). All of these factors, in addition to the complications posed by climate change and a lack of disturbance, account for the damage and lack of regeneration commonly noted among young aspen ramets at Smith Falls and the NRV.

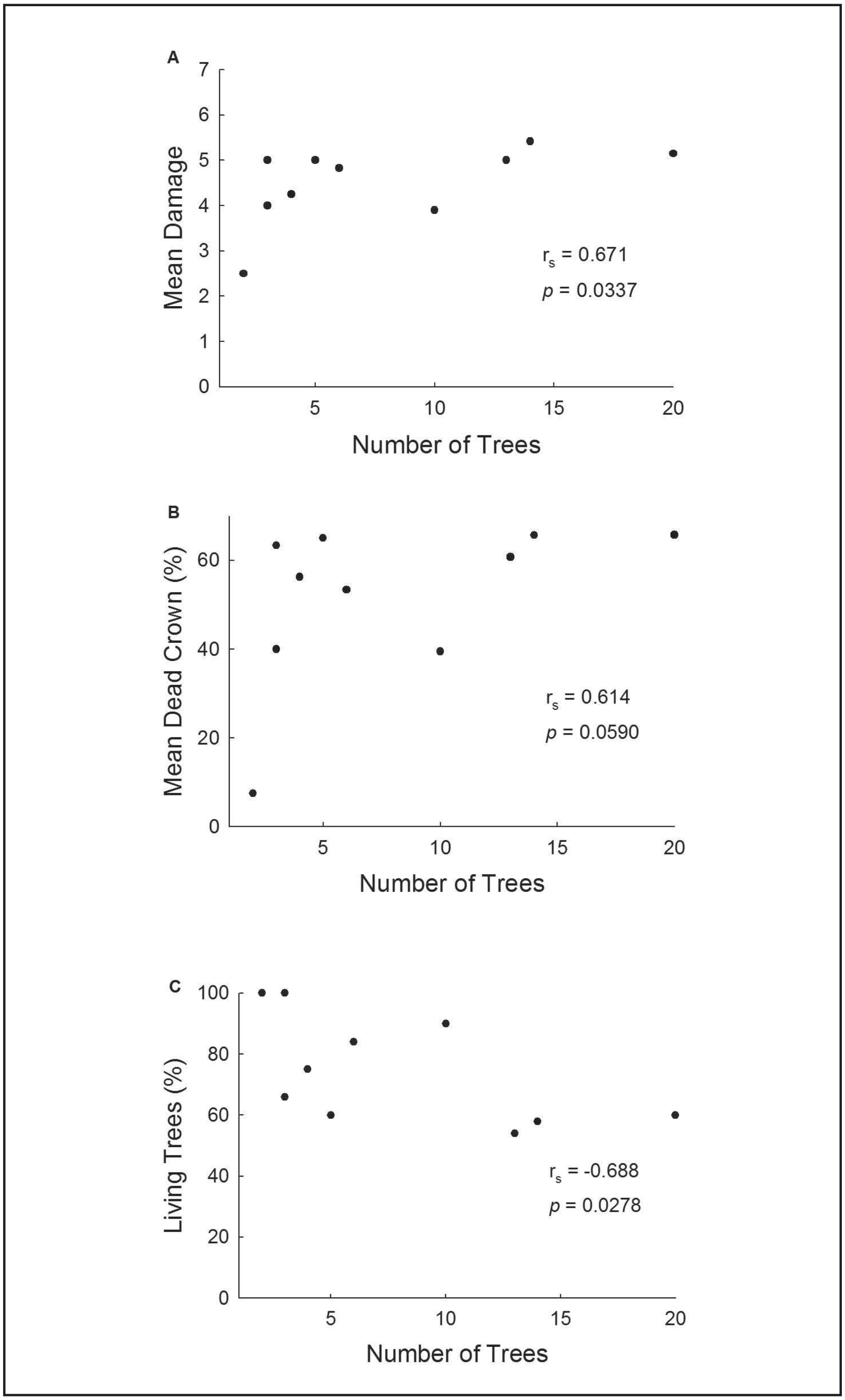

Figure 4. Stands with greater numbers of trees in 2013 showed significantly more damage than smaller stand populations as measured by (A) damage scale and (B) percent crown death, and (C) had a significantly lower percentage of living trees.

CONCLUSIONS

We hypothesized that this population would be weighted toward larger, older individuals due to a changing climate profile and a lack of disturbance at the site, but our findings told a somewhat different story. We found many younger, smaller trees in small stands, which were initially healthier than their counterparts, but also accrued the most damage over a 2-y period. In a healthy aspen population, this phenomenon could be viewed as a normal aspect of succession as abundant saplings compete for resources—but in this sparse population, the failure to recruit mature trees may act as a precursor to their extirpation. This likely reflects a major downturn in sucker recruitment over the last 25 y related to some combination of competition/shading from red cedar, a lack of physical disturbance, browsing by deer, and stress driven by climatic changes. Although recent management efforts have helped sucker and pole-class recruitment among *P.* × *smithii* (Robertson et al. 2018), it remains to be seen if this results in increased numbers of mature trees.

The disparity in health and mortality that exists between larger and smaller stands of aspens is an important outcome of this study, as it raises questions for management about what may be influencing such variability and what can be done about it. Older stands have had more time to spread and establish, resulting in large stands weighted toward large, dying individuals which, in the absence of a disturbance event, are

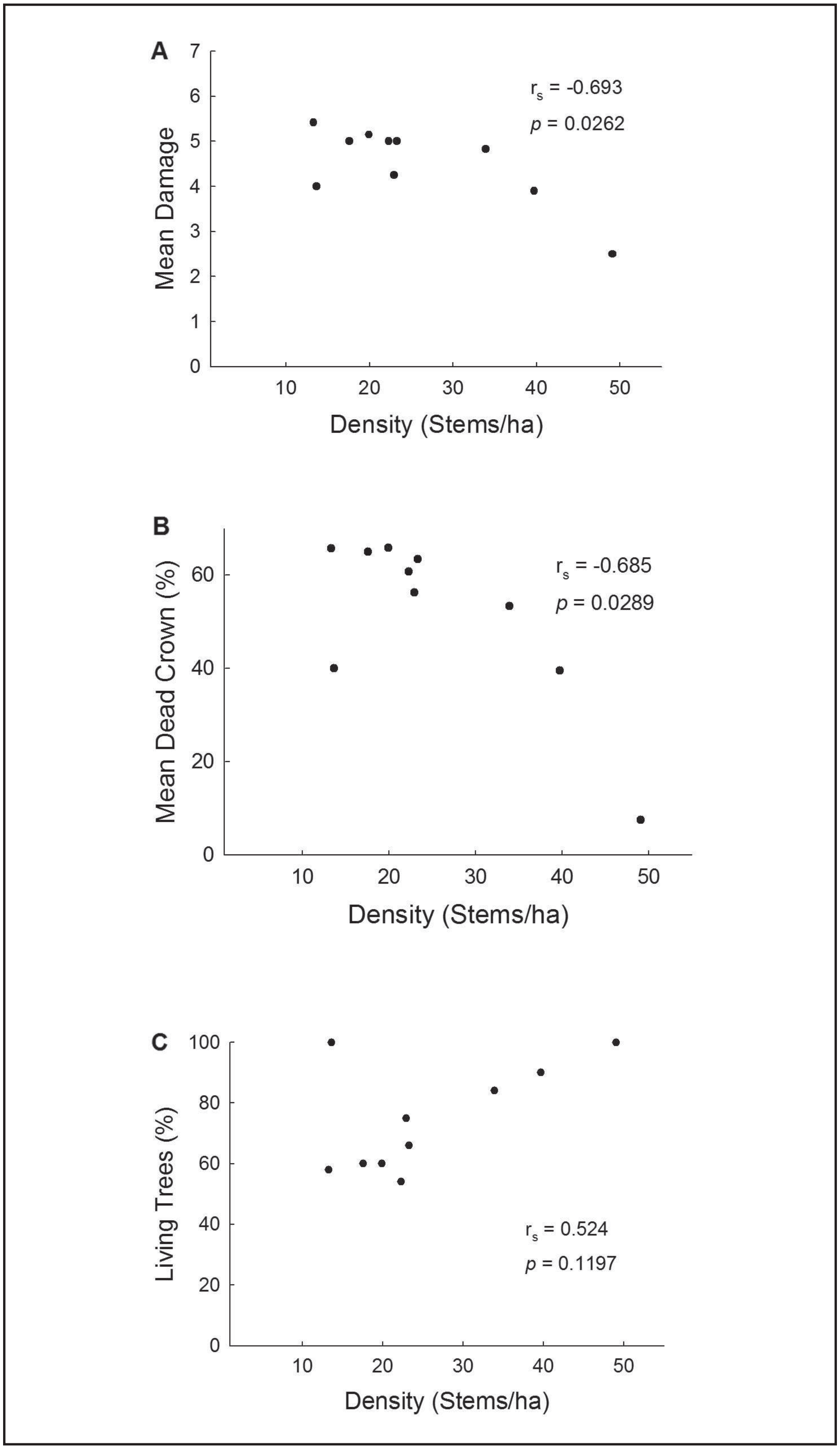

Figure 5. Density (m^2/ha) of *P.* × *smithii* populations in 2013 was negatively correlated with stand damage metrics. Denser aspen stands were associated with (A) lower damage scores, and (B) lower mean dead crown percentage. (C) Aspen density was weakly (non-significantly) positively correlated with percent of trees remaining alive in the stands.

being replaced by conifers (Eckenwalder 2010). Smaller stands represent the effects of recent disturbances and recruitment events, and are therefore more densely populated with younger, healthier trees. Although the successional nature of the species is likely also responsible for this disparity between stands, more concerning is the reduction in live individuals among all size classes in the 2015 resurvey, and in particular the significant increase in damage for the youngest trees. As even these youngest stands included some trees with heavy damage and over 40% crown loss on average, all of the aspen stands in the NRV are at risk if recruitment of young trees does not increase.

Management instituted by the stakeholders at Smith Falls State Park and the Niobrara Valley Preserve will likely have a positive impact on the aspen population. Clearing competitive red cedar from the smaller, younger aspen stands will encourage their spread and the recruitment of new mature boles. As a successional species, it should be noted that these small stands, which primarily occur along transitional zones on steep slopes and ridges, have the most potential to spread. Conversely, the larger stands may be less impacted by red cedar clearing. The abundance of old, unhealthy, and dead trees may be indicative of stands that are at the other end of the successional gradient. In the absence of a major disturbance event (fire, landslide), recruitment in these areas will continue to be hampered by competition from mature trees of this and other species, and herbivory by insects and deer.

In the future, proactive managers of this population should take advantage of the successional ecology of aspen and target the younger, smaller stands as areas for more clearing and the institution of other measures. Although elevation does not appear to be a factor influencing the health of *P.* × *smithii*, other environmental variables may be important and merit further study. The current paucity of young trees in these small stands is likely an effect of past competition from red cedar (which has now been cleared), browsing by herbivores, and a lack of disturbance events. Managers should orient their work toward increasing the stem density and overall basal area in these presently small stands.

NOTE: Refer to BioOne online for Supplementary Figure 1.

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