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Genetic and spatial structuring of *Populus tremuloides* in a mixed-species forest of southwestern Utah, USA

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ABSTRACT.—*Populus tremuloides* Michx. (aspen) is an iconic species of the southwestern United States, where it is known for its extensive clonality. The size of clones and pattern of clonal distribution within and among stands can provide important clues to the species' evolution and ecology, but there are very few studies that have conducted the type of sampling necessary to define these features. We examined the genetic composition and habitat associations of aspen in a mixed-species forest in Cedar Breaks National Monument on the Markagunt Plateau, southwestern Utah. Genetic analysis of 94 stems ≥1 cm diameter at breast height (dbh) selected from a population census of 2742 stems within a contiguous 13.64-ha plot revealed 2 spatially cohesive triploid genets and 2 diploid genets (all differing in 8 to 15 alleles). Aspen abundance within the 13.64 ha varied between 0 and 634 stems/ha across 8 distinct habitat types. Regenerating aspen stems (1 cm ≤ dbh < 5 cm) varied between 0 and 112 stems/ha, with higher levels of regeneration in habitats with greater aspen dominance relative to other tree species. Recent regeneration may have been stimulated by a *Dendroctonous rufipennis* outbreak in the 1990s, which killed a high proportion of *Picea engelmannii*. Even though the visual impression is of a single aspen clone, the 4 identified genets suggest a higher-than-expected level of genetic diversity in this mixed-species stand which may confer resilience to increasing climate variability and drought. Furthermore, aspen regeneration in areas of both low and high adult aspen densities show that these mixed stands can support vigorous aspen populations.

RESUMEN.—El álamo temblón (*Populus tremuloides* Michx.) es una especie emblemática del suroeste de los Estados Unidos, donde es conocido por su amplia capacidad de clonación. El tamaño de los clones y el patrón de la distribución clonal, dentro y entre los grupos, pueden proporcionar indicios importantes sobre la ecología y evolución de la especie. Sin embargo, existen muy pocos estudios que hayan conducido el tipo de muestreo necesario para definir dichas características. Examinamos la composición genética y asociaciones de hábitat de los álamos temblones, en un bosque de especies mixtas, en el Monumento Nacional Cedar Breaks en la meseta de Markagunt, al sureste del estado de Utah. El análisis genético de 94 tallos ≥1 cm de diámetro a la altura del pecho (DAP; DBH, por sus siglas en inglés) seleccionados de un censo poblacional de 2742 tallos, dentro de un lote de terreno contiguo de 13.64 hectáreas, reveló dos genetos triploides espacialmente cohesivos y dos genetos diploides (todos difirieron en 8 a 15 alelos). La abundancia de álamos temblones, dentro de las 13.64 hectáreas, varió entre 0 y 634 tallos por ha, a lo largo de ocho tipos de hábitat distintos. La regeneración de los tallos de álamo temblón (1 cm ≤ DAP < 5 cm) varió entre 0 y 112 tallos por ha, con niveles más altos de regeneración en hábitats con mayor dominancia de álamos temblones, en relación con otras especies de árboles. La regeneración reciente, puede haber sido estimulada por un brote del escarabajo *Dendroctonous rufipennis* en la década de los años 90 el cual eliminó a una alta proporción de *Picea engelmannii.* Aunque, la impresión visual es de un sólo clon de álamo temblón, los cuatro genetos identificados sugieren un nivel más alto del esperado de diversidad genética, en este grupo de especies mixtas, lo que le puede conferir resiliencia al aumento de la variabilidad climática y de sequía. Además, la regeneración del álamo temblón en áreas, tanto de baja como de alta densidad, de álamos temblones adultos, evidencia que estos grupos mixtos pueden sostener grandes poblaciones de álamo temblón.

Populations of *Populus tremuloides* Michx. (aspen) in the southwestern United States primarily reproduce asexually through root suckering, but seedling establishment is frequently documented in postfire landscapes where seedbed conditions are permissive (Barnes 1966, Kay 1993, Turner et al. 2003, Romme et al. 2005, Fairweather et al. 2014). In western North America, aspen populations tend to be a mixture of diploid and triploid clones, with a

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JAL orcid.org/0000-0002-2560-0710

greater proportion of triploid genets in unglaciated, drought-prone areas (Mock et al. 2012), which are primary landscape and climatic features of the southern portion of the species' range. Aspen is in decline in these areas because of increasing drought stress (Anderegg et al. 2012), but the degree to which the decline depends on habitat specificity or ploidy remains understudied. Furthermore, linkages between regeneration success and landscape positions (substrate type, aspect, and presence of other tree species) remain a key issue for conservation and reforestation efforts.

An understanding of local clonal dynamics with respect to ploidy levels and seedling establishment requires a fine-scale gridded sampling and genotyping approach, which is labor intensive and only rarely undertaken. Such an approach can identify clusters of small diploid clones, which can be an indication of past seeding events. Because triploids are expected to have greatly reduced fertility and problems associated with gene dosage regulation, we anticipate that there will be selection against clones producing high numbers of triploid seeds. Therefore, we expect that seed crops will be dominated by diploid seeds, and this prediction has been confirmed in nursery studies (Mock unpublished data). At the landscape scale, then, seeding events should produce a signature of clustered, smaller diploid clones and high numbers of clones within a stand. Mock et al. (2008) found these patterns using a gridded sampling approach in 2 different landscapes and demonstrated that larger clones in a landscape tend to be triploid, perhaps reflecting faster growth rates or positive selection (Mock et al. 2008). However, there is a need for a gridded or distributed sampling approach in other landscapes to corroborate these findings and to explore relationships between clonal patterns, landscape disturbance history, and biotic and abiotic landscape factors.

Here we used a distributed sampling design to study a 13.64-ha plot of contiguous forest in southern Utah to examine fine-scale heterogeneity in aspen clonal structure, triploidy, abundance, habitat association, and regeneration. Our objectives were to (1) describe the clonal and cytotype (diploid/triploid) structure of a contiguous aspen stand within a mixed forest, (2) examine the variability of aspen dominance and ploidy by habitat type, and (3) examine the regeneration of aspen by habitat type and genet.

METHODS

Field Sampling

The study site was the Utah Forest Dynamics Plot (UFDP), located in Cedar Breaks National Monument in southwestern Utah (latitude 37.66° N, longitude 112.85° W). The UFDP is a 13.64-ha forest dynamics plot affiliated with the Smithsonian ForestGEO network (Anderson-Teixeira et al. 2015, Lutz 2015, Lutz et al. 2018b) within which all 23,177 live woody stems ≥1 cm diameter at breast height (dbh; 1.37 along the main stem) have been identified, mapped, and tagged (Furniss et al. 2017). The UFDP has 8 habitat types differentiated by soil parent material and topographic position (Furniss et al. 2017), with all 8 habitat types showing positive or negative associations with the principal woody species (Table S3 *in* Furniss et al. 2017). Approximately 35% of the UFDP has a relatively uniform density of larger-diameter (≥25 cm dbh) *Populus tremuloides*, but the remaining 65% of the plot is mixed-species forest interspersed with aspen (Fig. 1). Grazing by nonnative ungulates has been excluded since 1935, two years after the establishment of Cedar Breaks National Monument. There have been no extensive fires since at least 1935. There are robust populations of *Odocoileus hemionus* (mule deer) and some *Cervus canadensis* (elk), both of which may be controlled by *Puma concolor* (mountain lion). The *Dendroctonous rufipennis* (spruce bark beetle) outbreak in the 1990s killed a high proportion of larger-diameter *Picea engelmannii* in the area (DeRose and Long 2007). Plant nomenclature follows Flora of North America (1993+).

In the summer of 2016, we performed a stratified random sampling of 96 out of the 2742 total *Populus tremuloides* stems ≥1 cm dbh within the UFDP. Using the locations of the 2742 stems, we sampled from across the range of slopes, aspects, and plant communities identified in Furniss et al. (2017) to achieve a representative sample of the distribution of the species in the UFDP. Sampled trees were selected to represent ten 5-cm-diameter classes (first diameter class 1 cm ≤ dbh < 5 cm). All 96 of the stems identified in the *a priori* stratification were successfully

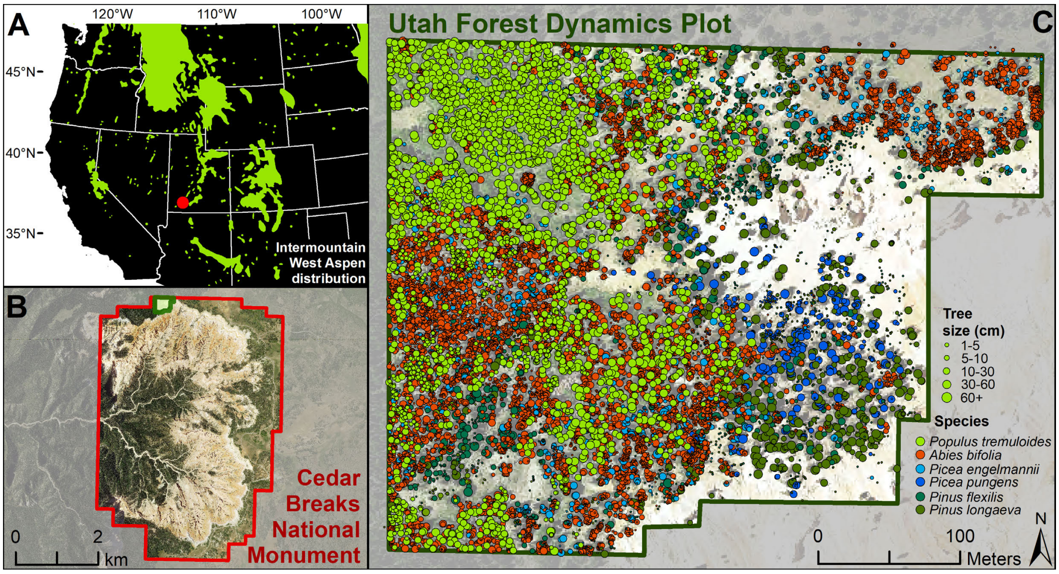

Fig. 1. The Utah Forest Dynamics Plot (UFDP) is located in southwestern Utah (A) on the north rim of Cedar Breaks National Monument (B). The forest within the UFDP is a mixed conifer/aspen subalpine forest dominated by 4 tree genera: *Populus, Abies, Picea,* and *Pinus* (C). Stem density and species composition is heterogeneous, driven primarily by habitat type. The green shading in panel A represents the distribution of *Populus tremuloides* in the Intermountain West (Little 1971).

sampled. Leaves for genetic analysis were collected from each of these trees and placed into paper envelopes submerged in containers of silica gel desiccant for preservation.

Laboratory Procedures

In the laboratory, sterilized metal hole punches (6.35 mm in diameter) were used to subsample dried leaves, with 2 punches taken from the outer edge of the lamina closest to the leaf tip in order to maximize the number of cell nuclei captured. We extracted genomic DNA from these leaf subsamples using a DNEasy 96 Plant Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions, and the extracted DNA was arrayed in a 96-well plate. In separate 96-well plates we amplified 10 microsatellite loci using the following PCR (polymerase chain reaction) conditions: 6.0 µL of MyTaq HS® Master Mix 2× (includes buffer and dNTPs), 2.5 µL of extracted DNA, 0.24 mM $MgCl_2$ (in addition to the 1.5 mM $MgCl_2$ already in the Master Mix), 0.36 µM of each primer, and 0.12 mg/mL of bovine serum albumin (BSA) with a total reaction volume of 12 µL. Thermocycling conditions were 95 °C for 2 min, followed by 30 cycles (94 °C for 30 s; a primer-specific annealing temperature for 40 s; 72 °C for 50 s) and a final extension step of 72 °C for 10 min. Primer-specific annealing temperatures were 50 °C (P10, P33, P76), 54 °C (W15), 55 °C (P14, P86), 56 °C (W16), 58 °C (W20), and 64 °C (W14, W17). Gel electrophoresis was used to estimate the amplicon sizes and concentrations.

Amplicons were multiplexed into 4 plates of compatible (nonoverlapping fragment size ranges) loci for fragment analysis (group #1: P10, W14, W16; group #2: P76, W15; group #3: P33, P86; group #4: P14, P17, W20). Analysis was performed by ETON Biosciences (San Diego, CA) on an ABI 3730xl sequencer (Applied Biosystems®). We used GeneMarker® software to bin and score fragment chromatograms. Each of the 10 loci had between 1 and 3 alleles, and 94 of the 96 samples were successfully genotyped.

Habitat Associations

Habitat types were defined by Furniss et al. (2017) based on geology (derived from Rowley et al. 2013) and aspect. Geology was used to delineate habitat types because there is a high degree of geologic diversity within the plot

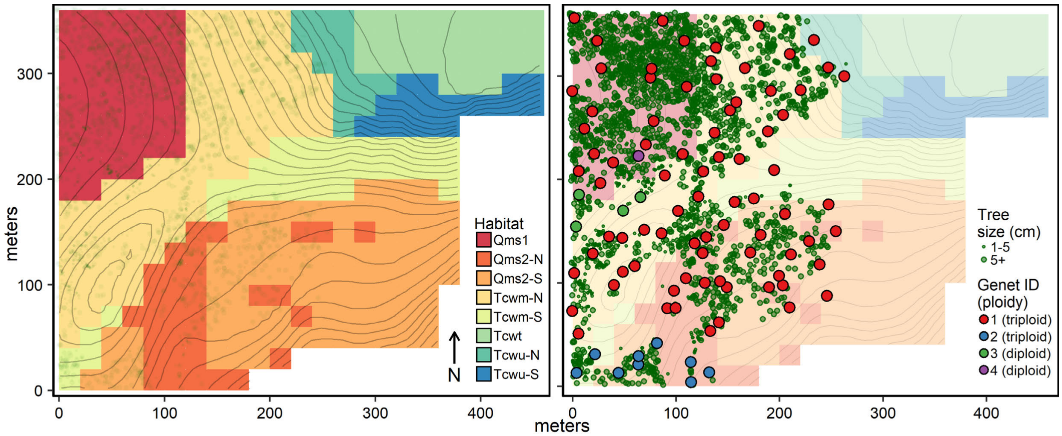

Fig. 2. Genet identification of 94 stems of *Populus tremuloides* in the Utah Forest Dynamics Plot. Dark green circles indicate the locations of all 2742 live *Populus tremuloides* stems ≥1 cm dbh. Contour interval, 5 m. Colored points represent the genet and chromosome count of the 96 *Populus tremuloides* individuals that we sampled. See text (this page) for a detailed explanation of geologic type codes. *N* and *S* indicate north- or south-facing habitats, following geologic code.

and because the geologic parent materials remain exposed due to the slow rate of soil development at high elevations and relatively recent landslides. Consequently, the geology in the UFDP is closely related to biologically relevant soil properties such as structure, depth, nutrient availability, and water-holding capacity. The plot contained 5 distinct geologic types, the 3 largest of which were further classified into northerly and southerly aspects to account for the importance of direct solar radiation in structuring high-elevation plant communities (Körner and Paulsen 2004, Halpern and Lutz 2013). The 5 geologic types included 2 areas of landslide deposits and 3 sedimentary layers that are part of the Claron formation. The 5 types were as follows:

Qms1 – landslide deposits that rest beneath Brian Head Formation material and the Tcwm layer

Qms2 – landslide deposits beneath the Tcwm and Tcwu layers

Tcwt – uppermost mudstone, siltstone, and sandstone unit of the white member of the Claron Formation

Tcwu – upper limestone unit of the white member of the Claron Formation

Tcwm – middle mudstone, siltstone, and sandstone unit of the white member of the Claron Formation

The selected habitat types present clear differences in various soil properties, which may translate into differences in cytotype performance. Although aspen clones may initially spread across habitat type boundaries, we expected long-term abundance to be dependent on local resources. For example, Tcwu and Tcwt, both being limestone-derived soils, likely have high pH and lower available minerals. Qms1, a well-mixed landslide deposit not including the white members of the Claron Formation, is likely more acidic (Sprinkel et al. 2010, Rowley et al. 2013). We compared the dominance of aspen relative to other species (percentage of stems and basal area) by habitat type, considering those other species having a density of ≥30 stems/ha ≥1 cm dbh. Smaller aspen stems (1 cm ≤ dbh < 5 cm) were considered to be recent regeneration, and larger stems (dbh ≥ 5 cm dbh) were considered to be established ramets. We tested whether the diameter distribution of *Populus tremuloides* varied by habitat type by using pairwise Kolmogorov–Smirnov tests ($\alpha = 0.05$) for each pair of habitats.

RESULTS

Clonal Structure

The 94 genotyped samples represented 4 distinct genets differing by 8 to 15 alleles. All samples that differed by 0, 1, or 2 alleles were pooled. The genet with the highest representation (genet 1t, 80 sampled stems) was

TABLE 1. Abundance and genetic composition of *Populus tremuloides* by habitat type in the 13.64-ha Utah Forest Dynamics Plot (UFDP). For each habitat type, the abundance of the 7 woody species with a density ≥30 stems/ha is shown. *N* and *S* indicate north- or south-facing habitats, following geologic code. Habitats Tcwt (1.2 ha) and Tcwu-S (0.7 ha) had no *Populus tremuloides.* Dominance indicates the percentage of the total stem density or basal area, respectively. Density is reported as stems/ha, and basal area is reported as m²/ha.

	Tcwm-S 1.3 ha		Qms2-S 3.4 ha		Qms2-N 1.2 ha		Tcwm-N 3.2 ha		Qms1 1.9 ha		Tcwu-N 0.6 ha	
Species	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area
Abies bifolia	277	3.70	1038	10.66	1531	18.98	1934	17.3	1485	12.11	357	3.52
Pinus longaeva	86	7.97	107	15.48	22	1.15	26	2.27	0	0	143	23.00
Pinus flexilis	49	2.80	47	2.16	84	3.27	116	5.54	5	0.01	162	8.30
Picea engelmannii	6	0.32	56	2.38	134	3.10	85	1.65	92	1.43	191	3.00
Picea pungens	61	3.56	81	6.01	33	2.84	3	0.08	1	0	0	0
Populus tremuloides	57	0.85	72	3.16	191	5.26	299	6.00	634	28.94	48	0.43
Populus tremuloides												
Dominance	9.9%	4.4%	5.1%	7.9%	9.4%	15.2%	11.9%	18.0%	28.6%	67.8%	5.2%	1.1%
Genets	1t, 2t		1t, 2t		1t, 2t		1t, 3d		1t, 3d, 4d		1t	

triploid (5 loci with 3 alleles), as was the second most sampled genet (genet 2t, 9 sampled stems, 3 loci with 3 alleles). Additionally, there were 2 diploid genets: one that was represented in our sample by 4 individual stems (genet 3d) and one that was represented by a single stem (genet 4d). The clonal boundaries of the 2 triploid genets were well delineated (Fig. 2), with the 3 diploid genets occurring within the larger triploid genet along a north-facing slope.

Abundance and Regeneration by Habitat Type

Aspen abundance varied by habitat type, with habitat types Tcwt (1.2 ha) and Tcwu-S (0.7 ha) not having any aspen stems. Relative aspen dominance varied from 5.1% to 28.6% (by stem abundance) and 1.1% to 67.8% by basal area among the 6 habitat types where aspen was present (Table 1). The diploid genets occurred in the 2 habitat types where aspen had the highest relative dominance (Tcwm-N and Qms1). The diameter distributions varied by habitat type (Fig. 3). The 2 habitat types with the highest proportion of aspen (Tcwm-N and Qms1) had a normal distribution of stems >5 cm dbh and had abundant regeneration in the 1–5 cm diameter class. Two habitat types (Tcwm-S, and Qms2-N) had aspen diameter distributions skewed toward smaller stems, although these habitats also had stems in the largest diameter class (50–55 cm; Fig. 3). One habitat type (Qms2-S) had a normal distribution of diameter classes with very little regeneration (3 stems/ha) in the 1–5 cm diameter class, and the diameter distribution of the final habitat type (Tcwu-N) was best approximated by a Poisson distribution. There was no difference between the mean elevation of regenerating stems and adults (both 3086 m).

DISCUSSION

In most aspen-dominated forests, the number of distinct clones is unknown and traditionally has been assumed to be quite low, with stands generally corresponding to individual clones or clonal boundaries being readily visible (Kemperman and Barnes 1976). Although the visual impression in each of the 4 seasons is of a single aspen clone, we identified 4 genetically distinct clones in our study site, indicating both genotypic and cytotypic diversity. This result is consistent with Mock et al. (2008) in suggesting that visual estimates can

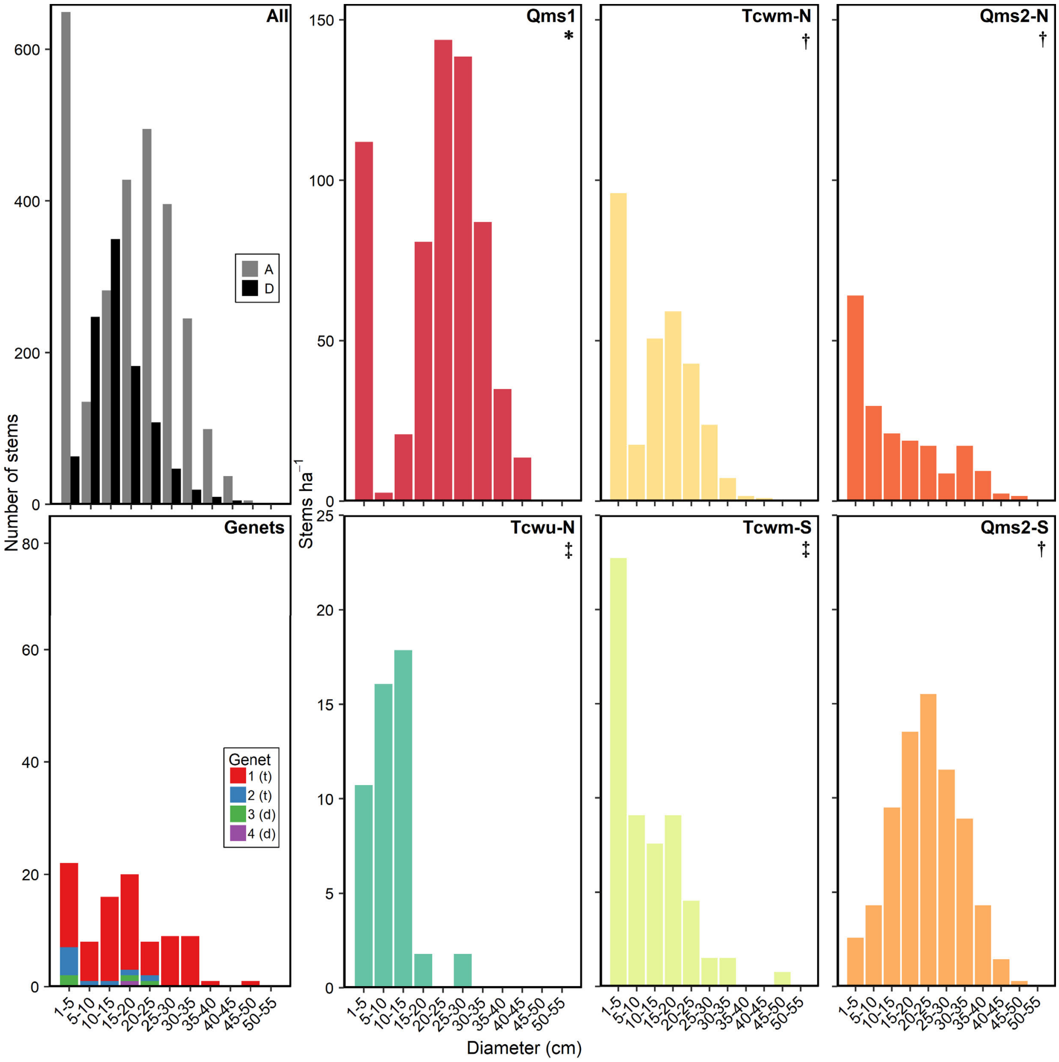

Fig. 3. Overall abundance of stems, sampled genets, and density by diameter class of *Populus tremuloides* for each habitat type where the species was found. Shading of density diameter distributions matches habitat type shading in Fig. 2. Symbols indicate statistically significant differences of diameter distributions between habitat types, determined by pairwise Kolmogorov–Smirnov tests (α = 0.05).

greatly underestimate genetic diversity. Genetic diversity is an important aspect of forest resilience, particularly in forests with clonal species, where both clone sizes and genetic heterogeneity can be highly variable (DeWoody et al. 2008). The co-occurrence of multiple genets within a single aspen stand suggests that genetic diversity is higher than would have been estimated under the assumption that stands represent single clones. Maintaining genetic diversity is an important objective for many land managers as it can contribute to increased resilience of aspen to future climate variability and increasing drought. Characterization of genetic diversity at the landscape scale could be an important metric for decision-making in forest management (Fischer et al. 2017 and references therein), but may be cost prohibitive at present using traditional genetic approaches. We concur with Madritch et al. (2014) that remotely sensed data with high temporal resolution may be a useful and economical tool for delineating extent and pattern of genetic diversity in forests.

The abundance of small stems in most habitat types indicates vigorous regeneration of *Populus tremuloides* at this site, even in the absence of fire. The site, located within Cedar Breaks National Monument, has experienced no commercial grazing for 80 years. Cedar Breaks National Monument does support vigorous populations of deer, with some visitation by elk, and the populations of both ungulates may be kept in check by the presence of mountain lion. Regeneration of small stems may also have been stimulated by resources released following the *Dendroctonous rufipennis* outbreak in the 1990s (DeRose and Long 2007; Fig 1 *in* Bentz et al. 2010), which killed many of the larger *Picea engelmannii* individuals within the UFDP (Table S2 *in* Furniss et al. 2017). In a broader study of the Markagunt Plateau, DeRose and Long (2010) also found a postoutbreak pulse of *Populus tremuloides* recruitment. However, their study found that advanced height growth of *Populus tremuloides* was limited by heavy ungulate browsing, whereas in the UFDP, the population of *Populus tremuloides* stems that has exceeded the browse threshold of 1.3 m is already high (Fig. 3). This study shows that aspen can recruit abundantly in the presence of native ungulate grazing and without fire (as compared to Rogers and McAvoy 2018). The most important factor associated with aspen recruitment in this study was fine-scale variability in habitat type, potentially emphasizing the importance of belowground nutrient and water resources to aspen regeneration.

Our findings are consistent with Mock et al. (2008), who demonstrated a tendency for larger clones to be triploid, possibly to due to a vegetative growth advantage (DeRose et al. 2015). Alternatively, triploidy in larger clones could suggest superior persistence and greater clonal age compared to diploids, perhaps due to increased heterozygosity, gene dosage effects, or protection from the effects of somatic mutations (Ally et al. 2010, Mock et al. 2008, 2012, Henry et al. 2015). The small number of diploid stems in our study plot suggests that diploid recruitment has not been historically common compared to asexual reproduction of the triploid genets. This apparent triploid vegetative superiority, however, may carry a increased vulnerability to drought mortality (Mock et al. 2012, Dixon and DeWald 2015, Greer et al. 2018), and this triploid advantage may not persist as droughts in the Intermountain West become more common and more severe (Prein et al. 2016).

The 2 habitats Tcwt and Tcwu-S had no aspen. The Tcwt habitat is the highest-elevation habitat within the UFDP and is occupied by dense clumps of *Picea engelmannii* and *Abies bifolia* (Table 1). The lack of aspen in this habitat type may be due to climate limitations (due to slightly higher elevation), competition from established trees and grasses (which grow in extremely dense clumps in this habitat type), or disturbance history (perhaps aspen has been outcompeted in the absence of disturbance). The Tcwu-S habitat is a steep talus slope, occupied primarily by *Pinus longaeva* and *Pinus flexilis.* This slope has poor soil development and relatively high levels of direct insolation, which suppress both suckering and seeding.

The density of small-diameter *Populus tremuloides* corresponded to the habitat associations identified by Furniss et al. (2017). Recruitment was highest in Qms1 and Tcwm-N habitats, which both had positive associations with *Populus tremuloides* overall (i.e., these were preferred habitats for *Populus tremuloides*). This recruitment pattern could indicate that the negative effects of conspecific competition are outweighed by habitat preference (Furniss et al. 2017, LaManna et al. 2017). There was a moderate amount of recruitment in Tcwm-S and Qms2-N habitats, which both had neutral associations with *Populus tremuloides,* and the lowest amount of recruitment was in Tcwu-N and Qms2-S, which were negatively associated with *Populus tremuloides.* The differing diameter distributions among habitat types may contribute to the high level of structural diversity present in the UFDP (Lutz et al. 2013, 2018a).

Recent research has begun to disentangle the complex effects of disturbance and climate on aspen population dynamics at the regional scale (e.g., Kulakowski et al. 2013), but we still lack a thorough understanding of how genetics and fine-scale habitat variability may influence aspen dynamics within a stand. We showed that genetic identity is an elusive characteristic but that genetic sampling may reveal unexpected patterns in the genetic structure of aspen stands. We also demonstrated that aspen populations respond to variability in habitat type and that this response influences the vigor of regeneration and overall diameter distribution of stems within a stand. Further research into the correlates between ploidy, genetic diversity, and specific environmental variables may illuminate which habitat attributes are the most important drivers of aspen distribution.

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