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Clonality and Dynamics of Leaf Abscission of Gambel Oaks at Small Spatial Scales in Utah

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The Intermountain West of the United States supports a mosaic of Gambel oak (*Quercus gambelii* Nutt.) clumps interspersed with grassland. Both the tree and shrub forms of Gambel oak are typically found in distinct clumps that have often been presumed to be single clones, although quantitative evidence to support this is minimal. We examined the patterns of clonality within and between oak clumps and explored the variance in phenology of leaf abscission within and among clones and clumps in a study site in the Wasatch Mountains, Utah, USA. Using amplified fragment length polymorphism analysis, we genotyped multiple stems within 10 clumps of Gambel oaks in Red Butte Canyon. Nine of the 10 clumps were monoclonal (each a single distinct genet). The 10th clump was composed of 2 genets. To characterize the genetic influence on leaf abscission phenology, we compared the timing of abscission of individually marked leaves among genets, ramets, and branches. Of these three levels of organization, genet membership had the greatest influence on timing of leaf abscission, and branch membership had the smallest influence. Our results suggest that clonal diversity may be an important metric of phenotypic and ecological diversity in Gambel oak landscapes.

Keywords: genet, ramet, abscission, Gambel oak

Plant communities often comprise genetic mosaics at multiple spatial scales because species in the communities reproduce both sexually and asexually. In asexual reproduction, vegetative structures of parental genotypes (genets) produce genetically identical individuals (ramets) capable of independent growth and reproduction. However, clonal boundaries can be difficult to define on site. Clonality is more reliably identified with molecular techniques (Arnaud-Haond et al. 2005, 2007). Many woody species reproduce clonally, e.g., aspen (*Populus tremuloides* Michx.), black locust (*Robinia pseudoacacia* L.), and sweetgum (*Liquidambar styraciflua* L.) (Barnes 1966, Barrett et al. 1990, Wendling et al. 2010), and dual reproductive modes can provide advantages for perennial species (Silander 1979). Nonetheless, clonal reproduction has limitations and is associated with reduced genetic diversity and adaptive potential (Frankham 1998, 2002).

Individual ramets within a genet may vary phenotypically due to mutation accumulation, epigenetic mechanisms, or spatially varying environmental modulators (Klekowski 1984, Jablonka and Raz 2009). Phenotypic variation within or among genets may have ecological importance for herbivory, nutrient cycling, and facilitation of other species (Whitham et al. 2003, Madritch and Lindroth 2011, Davies et al. 2014). Therefore, a key question in consideration of woody plant clonality is how ecological and phenological trait variances are partitioned among genets (clones) versus ramets (stems). The answer, which is probably species and trait specific, also has implications for landscape-level phenological patterns and ecological processes. For *P. tremuloides,* for example, many phenological traits (leaf emergence, leaf coloring, and leaf abscission) are strongly correlated within genets (Barnes 1975, Kanaga et al. 2008).

Gambel oak (*Quercus gambelii* Nutt.) is widely distributed in the intermountain West and is commonly found between 1,700 and 2,300 m, particularly in areas of Arizona, Colorado, New Mexico, and Utah (Clary and Tiedemann 1993). Gambel oak is a member of the white oak group (Abella 2008), in which growth form varies from a tall shrub to a small tree. Stands may occur as dense shrubby patches 1 m tall or as widely spaced trees up to 23 m tall (Clary and Tiedemann 1993). After fire, Gambel oak regenerates quickly from adventitious buds on lignotubers and rhizomes, providing important wildlife habitat cover and food (acorns and foliage) for various species such as Abert's squirrels, band-tailed pigeons, Merriam turkeys, harlequin quail, javelina, whitetail deer, mule deer, and elk (Reynolds et al. 1970, Tiedemann et al. 1987, Clary and Tiedemann 1993).

Sexual reproduction in Gambel oak appears to be episodic, typically with limited recruitment after exposure to fire, herbicide applications, or woodcutting (Tiedemann et al. 1987). However,

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Gambel oak also regenerates asexually, producing numerous sprouts from primordial buds on their rhizomes and lignotubers (Tiedemann et al. 1987). Gambel oaks frequently occur in clumps that range from 1 to 20 m in diameter and only rarely exceed 50 m in diameter (Kumar and Rogstad 1998). These clumps are presumed to consist of genetically identical ramets originating from underground systems of lignotubers and rhizomes (Tiedemann et al. 1987, Schnabel and Hamrick 1990). However, such clusters could also arise from multiple seeds deposited near each other, cached by rodents or birds. Ellstrand and Roose (1987) examined 21 plant species known to be clonally propagated with extremely limited sexual reproduction and found that asexual populations were frequently as genotypically polymorphic as sexually propagated ones and that stands were frequently polyclonal. In aspen stands that were previously thought to consist of one or only a few genets, researchers have found high levels of genet richness (DeWoody et al. 2008). Similarly, in some oak species, tree clusters were frequently composed of multiple genotypes, presumably due to seed caching or short seed dispersal distances (Montalvo et al. 1997, Mayes et al. 1998).

Assessing the clonality of Gambel oaks contributes to our understanding of the genetic component of critical plant life history traits, such as foliar dynamics. Leaf senescence and abscission are ordered series of events influenced by both environmental and genetic factors that allow trees to conserve resources, prepare for a dormant period, and shed inefficient tissues in preparation for aboveground dormancy. A major factor that influences nutrient cycling in a forest community is the return of nutrients to the soil from leaf litter. The timing of leaf abscission and leaf fall may play an important role in modifying the chemistry, the rate, and/or the quantity of nutrients returned to the soil and therefore affect the function of the forest community (Niinemets and Tamm 2005). The timing of leaf abscission can be highly variable among plants in a population and even among leaves within a plant (Waddell et al. 2001).

Leaf senescence is typically initiated by environmental factors such as disease, nitrogen deficiency, light limitation, shortening of day length, drought (Buchanan-Wollaston 1997), and local climate (Chuine et al. 2000). There is also a genetic component to leaf senescence timing in many species, e.g., *Arabidopsis* (Lim et al. 2007), *Populus* (Ingvarsson et al. 2006), and possibly *Quercus* (Alberto et al. 2013). For many plant species, phenological traits are highly heritable and closely linked to growing season patterns.

In this study, we use genotyping to describe clonal richness in Gambel oak clumps, and we describe leaf abscission within and between genets and clumps. Our research addresses whether each clump of Gambel oak represents a single genet and how the timing of leaf abscission varies within and between genets. Our research tests the hypotheses that each clump of Gambel oak is a distinct genet and that the timing of leaf abscission differs among genets.

Materials and Methods

The study was conducted in Red Butte Canyon in the Wasatch Mountains, east of the University of Utah in Salt Lake City, Utah (40°46.626 N, 111°49.167 W). In June of 2013, we collected leaf samples from 10 clumps of pure Gambel oak, along a transect of ~500 m in length along an elevational gradient from 1,660 to 1,790 m, beginning 2 km from the access point of the road (to avoid disturbance from vehicles), and continuing in a north-northeast direction. Along the transect, we selected the nearest clumps we encountered that fell within a size range between ~20 and 50 m in diameter. Dimensions of sample trees and clumps are provided in Table 1. Within each clump, three trees were selected in the middle of the clumps to avoid impacts from exposure to wind and potential grazing by ungulates. The trees selected were also of similar height and aspect. Within each tree, three branches were selected from the central area of the tree crown. On each of these branches, leaf samples were collected from branchlets that emerged at the approximate midpoint of each branch (between the junction with the trunk and branch tip) for genetic analysis and monitoring of leaf abscission. The spatial coordinates for the center of each clump were recorded.

Table 1. Dimensions of Gambel oak (*Q. gambelii* Nutt.) clumps included in the present study.

Dimensions	Minimum	Maximum	Mean
Clump diameter (m)	7.2	18	12.6
Clump width (m)	8.5	24	15.9
Distance between clumps (m)	28	107	64
Mean height of ramets within clump (m)	1.0	2.1	1.5
Mean diameter of ramets within clump (m)	0.04	0.07	0.05
Height of ramets tested (m)	1.0	2.3	1.63
Diameter of ramets tested (m)	0.03	0.08	0.07
Average clump area (m^2)	29	198	110
Average stem density (stems/m^2)	1.6	5.5	3.0

All clumps are along a 500-m transect in northern Utah. Ten clumps were tested with three trees being tested within each clump.

Leaves were collected from a total of 30 sample trees for genotyping. Each tree was represented by three leaves, each from a different branch (90 samples total), and the three leaves were treated as replicates in subsequent DNA extraction, polymerase chain reaction (PCR) analysis, and scoring. Samples were preserved in a silica gel desiccant, and DNA was extracted using a QIAGEN DNeasy 96 Plant Kit. DNA quality and quantity were assessed on a 0.7% agarose gel stained with GelRed. We used amplified fragment length polymorphism (AFLP) analysis to characterize multilocus genotypes on all samples (Mueller and Wolfenbarger 1999). Eight of the samples were unsuitable either because of low quantities of extracted DNA or failure to amplify at some stage of the AFLP analysis. The remaining 82 samples represented all sample clumps and sample trees, with 1–3 samples per tree.

We scored 101 polymorphic AFLP loci across all 82 samples using Genographer 2.1 software (Benham 2001). Scores were assigned without reference to sample identity. Using 5 replicates of leaf samples from the extraction stage, we found the error rate to be low (0 mismatches for 4 of them and 3 mismatches for the other). The genetic sampling design of multiple leaves per clump and per tree also provided extensive replication. All final genet identities (see below) were identical within sample trees. Multilocus genotypes (MLGs) of the same genet may differ because of either somatic mutation or technical/PCR error. The error from these sources is expected to be much lower than the mismatches among MLGs due to membership in different genets that originated sexually. A distribution of the number of mismatches present in all pairwise individuals was constructed to establish a threshold for identification of unique genets (Meirmans and Van Tienderen 2004). Genetic distances between genets were represented as the number of mismatches, and the matrix of these distances was represented in a 2-dimensional principal coordinates (PCoA) plot using GenAlEx software (Peakall and Smouse 2006, 2012).

For the abscission study, the 10 uppermost leaves on each of the three branches selected within each ramet were numbered with an impermeable marker to keep track of the cohorts of leaves. From

Table 2. Proportion of leaves remaining in Gambel oak (*Q. gambelii* Nutt.) ramets by clump, clone, and observation date.

Date	Clump designation												
	1 (I)	2 (F)	3 (K)	4 (B)	5 (J)	6 (E)	7 (H)	8 (C)	9 (G)	10 (A)	10 (D)	Mean	SD
Sept. 18, 2013	99	98	99	99	99	98	91	92	99	98	100	97.4	3.0
Sept. 30, 2013	97	93	99	99	97	81	90	69	97	96	97	92.3	9.3
Oct. 8, 2013	96	87	93	86	87	68	54	42	92	92	97	81.3	18.4
Oct. 18, 2013	66	43	68	71	74	49	8	10	84	58	93	56.7	27.5
Oct. 22, 2013	26	7	54	40	52	23	0	1	37	21	60	29.2	21.2
Oct. 29, 2013	3	0	2	0	4	0	0	0	0	0	0	0.8	1.5
Nov. 12, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0

The clumps are listed in order along a 500-m transect. The letter in the parentheses represents clone.

Sept. 18, 2013 to Nov. 12, 2013, we counted the number of remaining leaves at intervals ranging between 5 and 13 days (mean = 9.5 ± 3.42 d) to determine the rate and timing of leaf abscission.

We documented differences in leaf abscission at three levels of biological organization: genet, ramet (nested within genet), and branch (nested with ramet and genet). Using JMP 10.0.2, we conducted survival analyses on pooled and split data. We first conducted Wilcoxon survival analysis at the genet level by pooling all leaves within genets. We next tested for tree differences by analyzing the data individually for each genet, with ramet as the independent variable (data for all branches were pooled within a ramet). One genet [10(D)] was only represented by one ramet, so we could not test for ramet differences within this genet. Last, we tested for branch differences by analyzing each ramet individually with branch as the independent variable.

We also fit a nested parametric survival model including all variables to test for differences in time of leaf abscission for dates between September 2013 and November 2013 (see Table 2 for dates). The predictive powers of independent variables were compared using the likelihood ratio χ^2 statistic, with higher likelihood ratios being indicative of more predictive power (Whitlock and Schluter 2009).

Because abscission rates can be affected by spatially varying environmental factors (e.g., elevation) and genetic factors, we characterized the correspondence between matrices of genetic (mismatches), geographic (m), and abscission distances in a series of Mantel tests (Mantel 1967) using GenAlEx software (Peakall and Smouse 2006, 2012). In all pairwise tests, the probability of the observed values was determined using 999 permutations of matrix elements to construct a matrix of pairwise differences comparing the differences in abscission of the studied genets for the dates of Oct. 18 and 22, 2013, which captured the greatest variance among genets and when all genets had some leaves remaining (Table 2). Abscission rate (phenotypic) distances between pairs of genets were calculated as the difference in the percentage of leaves remaining (the percentage averaged across branches within genets).

Results

The AFLP mismatch distribution shows two clear groups of pairwise mismatch quantities: those differing by between 1 and 7 mismatches and those differing by 19–50 mismatches (Figure 1). Based on these data, we considered samples differing by 0–7 allelic mismatches to be members of the same genet. All samples that differed by at least 19 mismatches, well above both the level of mismatches noted in replicates and the somatic mutation rate observed in the mismatch distribution, were considered individual genets (Figure 1). Among genets, mismatches were also distributed bimodally, suggesting the presence of a group of closely related genets (e.g., half-siblings) within the sample set. Nine of the 10 clumps were represented by single, unique genets, and clump 10 (at the northernmost end of the transect) consisted of two genets (A and D). Genetic distances between these genets are illustrated in the PCoA plot (Figure 2).

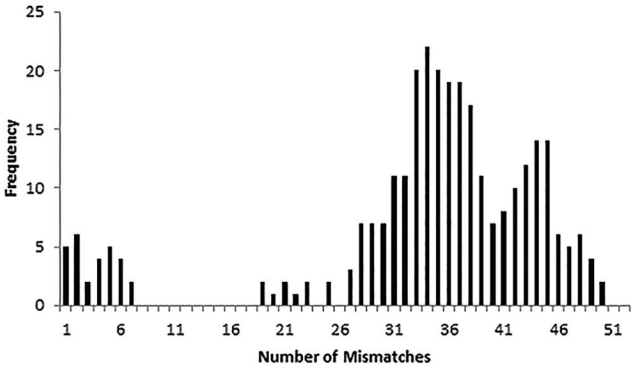

Figure 1. Distribution of AFLP mismatch frequencies in *Q. gambelii* genets.

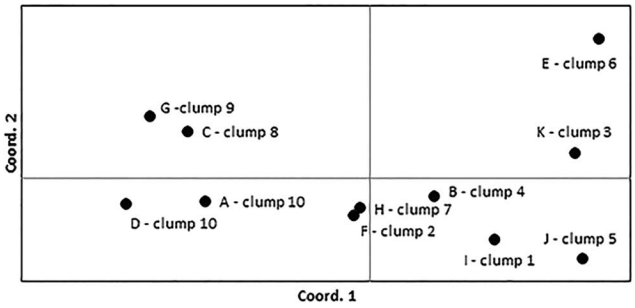

Figure 2. PCoA of *Q. gambelii* genets (letters) and clump numbers. The first axis captured 18% and the second axis 14% of the variance in the matrix.

Abscission data by date, clump, and genet are presented in Table 2. When data were pooled within genets across the dates Sept. 18–Nov. 12, 2013, there was a significant difference in time to leaf abscission among genets (Wilcoxon survival analysis; $P < 0.0001$). When each genet was tested individually, 8 of 10 genets exhibited significant effects of ramet on timing to leaf abscission ($P < 0.05$) for the dates listed in Table 2. When ramets were tested individually, 20 of 30 ramets exhibited significant effects of branch on timing to leaf abscission ($P < 0.05$) for the dates in Table 2. The nested parametric survival model showed that genet, ramet, and branch all appear to have an impact on timing of leaf abscission (Table 3).

Table 3. Timing of abscission for genet, ramet, and branch, using nested parametric survival data in Gambel oak (*Quercus gambelii* Nutt.).

Source of variation	*df*	Likelihood ratio χ^2	*P*
Genet	10	468.97	<0.0001
Ramet	19	289.07	<0.0001
Branch	59	376.84	<0.0001

Table 4. Results of Mantel testing for correlations (*R*) and probabilities (*P*; 999 permutations) between pairwise matrices of geographic distance, genetic distance, and abscission distance in Gambel oak (*Q. gambelii* Nutt.).

Pairwise distance matrix 1	Pairwise distance matrix 2	*R*	*P*
Geographic	Genetic	0.234	0.023*
Geographic	Phenotypic (Oct. 18, 2013; JD 2456583.5)	−0.050	0.388
Geographic	Phenotypic (Oct. 22, 2013; JD 2456587.5)	−0.060	0.419
Genetic	Phenotypic (Oct. 18, 2013; JD 2456583.5)	−0.369	0.004*
Genetic	Phenotypic (Oct. 22, 2013; JD 2456587.5)	−0.249	0.023*

Abscission distances were calculated using the difference in proportion of leaves retained. Dates are listed in standard form and also as Julian Dates (JD).
*Significance at $P < 0.05$.

However, the likelihood ratio χ^2 statistic was highest for genet (Table 3), suggesting that this variable had the strongest influence on leaf abscission timing.

The 11 clones showed a marginally significant positive relationship between geographic distance and genetic distance, suggesting that the more closely related clones are spatially proximal (Table 4). There was a nonsignificant relationship between geographic distance and abscission distance for the two observation dates showing the greatest variance among clones (Oct. 18 and 22, 2013) (Tables 2 and 4), suggesting that abscission distances were not due to the slight elevational gradient present. There was a significant negative relationship between genetic distance and abscission distance (Table 4), suggesting that the more closely related genets were unexpectedly distinct with respect to abscission timing.

Discussion

The clonality of long-lived sedentary taxa, such as trees, is an important component of landscape level biodiversity and is useful for studying the drivers of important plant life history traits. Gambel oak is known to be a clonally propagated species (Tiedemann et al. 1987, Abella 2008), but estimates of the distribution and extent of clonal richness differ among studies, probably due to variances in local and regional climates, communities, soils, and methods of ascertaining clonality. In our study, 9 of the 10 Gambel oak clumps were monoclonal, and 1 clump consisted of two distinct clones. Our findings with respect to clump and clone sizes are consistent with previous work in Colorado, which documented low numbers of genets growing within distinct clumps 1–20 m in width and which demonstrated that genets exceeding 50 m in diameter were uncommon (Table 1) (Kumar and Rogstad 1998). In contrast, a study in central Utah showed that herbicides were translocated via roots between Gambel oak clumps up to 24 m apart, suggesting that genets extended beyond distinct clumps (Van Epps 1974). However, root grafting in Gambel oak could also explain the transfer of herbicides between clumps (Tiedemann et al. 1987). In our small sample, no genet occupied more than one clump, suggesting the possibility that in a patchy landscape, the number of clumps may serve as a coarse estimate of genet diversity in Gambel oak. However, the correspondence between genet and clump should be investigated at larger landscape scales, and spatial autocorrelation (i.e., relatedness) should be considered.

Leaf abscission phenology is a heritable trait in Gambel oak that may influence population-level variation in biomass production, acorn production, and cavitation susceptibility and may even drive landscape-scale variation in soil properties, nutrient cycling, and insect communities. Leaf abscission timing in our study was highly significantly different among genets, ramets, and branches. Among these three main sources of variation, the likelihood ratio χ^2 value was highest for genet. The predictive power for abscission rates was highest for genet and lowest for ramet. Because most clumps were also individual genets, variations in local environmental conditions may be a confounding factor for genet and should be more closely examined. However, there was no relationship between geographic distance (congruent with elevational distance) and abscission distance, and there were no obvious differences among the sites occupied by clumps. Small sample size is a likely explanation for the observed negative correlation between genetic distance and abscission distance.

For other clonal tree species such as *Populus tremuloides*, ecological traits appear to differ among genets (Kanaga et al. 2008), creating a mosaic of variance in ecosystem functioning. Forest stand and wildlife indicators established by the US Department of Agriculture to evaluate the overall health of a forest ecosystem include crown condition, seasonal growth rates, tree mortality, frost susceptibility, and soil condition (Stolte et al. 2002). We suggest that genet richness and diversity should also be considered in the case of highly clonal species such as Gambel oak in the assessment of ecosystem variability at this spatial scale.

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