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Variability of whitebark pine (Pinus albicaulis Engelm.) leaf traits in the Great Basin Desert

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Abstract: Whitebark pine are valued for the ecosystem services they provide in subalpine forests of the western United States and have been declining across their range. This project quantifies two leaf traits of contemporary and historical populations (sites) of whitebark pine within the Great Basin. Characteristics of historical herbarium specimens were compared against samples collected in the 2018 field season of four different populations of whitebark pine within the Great Basin and the eastern Sierra Nevada. We asked how these populations differed from each other. Little change was observed through time for any of the sites, but leaf trait values were different among populations. The Jarbidge site within the Great Basin showed the most different leaf trait values, with smaller leaf mass per area and fewer leaves than other sites, in both historical and contemporary samples. Our research suggests there are differences among populations that may reflect important differences among growing conditions, genetic variation, or a combination of these factors. Additional research is needed to determine what is driving variation among whitebark pine within the Great Basin.

1 Introduction

Whitebark pine is valued for its ecosystem services and the wildlife habitat it provides (*1*). It has an expansive range in high elevation western North American forests (*2*), but whitebark pine has been declining across its range due to a variety of interconnected mortality agents including white pine blister rust (*3*), the mountain pine beetle (*4*, *5*), and drought (*6*). The influence of drought is particularly crucial because it can cause direct mortality (*6*), lead to decreased tree vigor, and exacerbate other sources of mortality (*7*, *8*). The effects of drought are especially felt in environments where resources are limited, such as sub-alpine ecosystems (*9*). However, the influence of drought on whitebark pine adaptation has not been fully examined.

The effects of drought on plants are measured by changes in their ecophysiology (*10*, *11*). These processes can be inferred through leaf traits such as leaf quantity (*12*), and leaf mass per area (*13*). Previous studies have shown that leaf traits vary through time in both annual (e.g., Ref. (*14*)) and perennial species (e.g., Ref. (*15*)), and leaf morphology is known to respond to drought (*12*). Understanding the variability of a species across environmental gradients is a key first step to understanding whether populations are adapted to their local environments (*16*) and measuring the variation in traits over time can indicate whether morphology is changing in response to factors such as drought or harvest (*17*). Leaf traits are easy to measure on herbarium specimens, allowing for analysis through time, even of long-lived perennials.

Determining the distribution of trait variation across populations can better guide restoration efforts (*18*). Whitebark pine populations are locally adapted across geographic areas with traits related to cold adaptation, and current restoration practices for whitebark pine utilize seed transfer guidelines based on climatic factors (*19*). These practices include moving genetic stock across environments that do not differ by more than 1.0°C in mean temperature (*19*). Whitebark pine habitats also differ in a variety of other environmental conditions such as vapor pressure deficit and precipitation (*20*), which haven't been studied for this species. Work to-date on trait distribution in whitebark pine has not fully incorporated populations within the Great Basin, and additional drought-specific traits may be of interest. For example, leaf number is known to decrease as a way for trees to manage water stress (*21*), while leaf mass per area (LMA) is shown to be higher in more drought-resistant plants (*22*). The relation-

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ship between LMA and drought may be more complicated. For example, LMA was documented to decrease in Scots pine (Pinus sylvestris) during drought-induced mortality events (*23*).

The objectives of this research were to ask the following questions: (1) Do leaf quantity and LMA differ within contemporary whitebark pine populations in the Great Basin and the Sierra Nevada mountains? And (2) have leaf quantity, and LMA changed through time? We predicted that populations would differ and that regions with greater water limitation would have lower leaf quantity and higher LMA. We expected that leaf quantity would decrease over time in areas experiencing climate warming, and would increase in areas getting wetter over time, with LMA showing the opposite pattern. We were also interested in whether populations differed in their ability to change in these leaf traits over time, which might indicate a higher degree of plasticity within certain populations and better predict success after seed transfer (*16*).

2 Material and methods

2.1 Population selection

We studied four populations of whitebark pine: Mount Rose (MR), Eastern Sierra (ES), Ruby Mountains (RM), and Jarbidge (Jar). We chose populations based on the availability of historical specimens at the University of Nevada, Reno herbarium (Appendix Table 2). Samples were identified using the Intermountain Region Herbarium Network (*24*) and selected based on specimen location. Each population, defined as a different mountain range, contained a minimum of three historical samples collected at least ten years before sampling. The date of collection for specimens ranged from 1912 – 2006. While these historic specimens varied greatly in age, we included all of them due to the limited data available for historic measurements. Geographic locations were determined based on the collection information provided in the descriptions of the specimens. These locations created a starting point for identifying the contemporary population in the same locality.

2.2 Field sampling

To determine the target tree branch size for field sampling, we measured the stem diameter of herbarium specimens at the nadir of each sample, near the point where the sample was removed from the tree. We then averaged the diameters within populations to create a target diameter for contemporary sampling, which were collected at each of the four mountain ranges based on this measure. Averaging the stem diameter was done to reduce sampling biases based on branch age, and to conduct the most accurate comparison of modern samples to historical specimens. Trees (n = 30 per site) were chosen randomly within a 5-km radius. Two samples were collected per tree based on the stem diameter at varying locations of the tree. Global Positioning System (GPS) points were recorded at every replicate tree (Appendix Table 1). Samples were then stored in a plant press for at least one week to preserve leaf tissue.

2.3 Train measurements

Leaf quantity and LMA were estimated based on methods used by Abrams et al. (*10*). We counted every fascicle for contemporary specimens and multiplied the final count by five, assuming every fascicle had five needles. Individual needles were counted for herbarium specimens due to fascicles of herbarium specimens not being readily visible without destructive sampling. The needle count of herbarium specimens was rounded up to the next multiple of five, assuming that needle count would be a multiple of five. LMA measurements were conducted on both contemporary and historical specimens. Needles were randomly pulled from a bag of contemporary samples to ensure random selection. The herbarium director permitted us to remove a single needle from the specimen mounts; this was done for all but one delicate specimen (Appendix Table 2). If able, needles were selected at random from a small pocket at the bottom of the herbarium sheet where residual material was stored. All leaves were oven-dried for two days at 40°C before measuring LMA, similar to work by Hultine & Marshall (*25*).

2.4 Climate data

Precipitation and vapor pressure deficit (VPd) data were gathered from the PRISM Climate Group (*20*) for each location and used as a proxy for drought stress. The trends of 30-year average precipitation were used to assess change over time for each population.

2.5 Data analysis

All of our analyses were performed using R statistical software (*26*). ANOVA was used to compare contemporary populations based on LMA and leaf quantity metrics. T-tests were used to compare LMA and leaf quantity through time within the same population. For the purpose of a pairwise statistical test, age was categorized as either "contemporary" or "historical." These data were compared against the leaf trait values for the corresponding population.

3 Results

Do leaf quantity and LMA differ within four contemporary populations of the Great Basin and eastern Sierra? Precipitation was variable across the four populations (Table 2). The Mount Rose population had the highest 30-year average precipitation, and Jarbidge had the lowest average rainfall. However, the VPd was less variable and showed no apparent differences among populations (Table 2). Precipitation was increasing at three sites, and decreasing at one.

Contemporary populations differed in leaf traits, with the Jarbidge population varying the most other populations (Figure 1). Average leaf quantity per replicate at Jarbidge (n = 613) was significantly lower than other populations (Jar-ES p = 0.0110; Jar-MR p < 0.0001; Jar-RM p = 0.0001). The other populations did not differ significantly from each other in average leaf quantity (Figure 2). Similarly, the LMA measurements for Jarbidge (0.0229 g/cm^2) were lower than the other populations (Jar-ES p < 0.0001; Jar-MR p < 0.0001; Jar-RM p = 0.0491). Additionally, the Ruby Mountain population had slightly lower LMA than the Eastern Sierra population and was significantly smaller than the Mount Rose LMA measurements (RM-MR p = 0.0146).

Do leaf quantity and LMA change through time within four populations of the Great Basin and eastern Sierra? Of the four populations and two traits, only one leaf trait in one population exhibited change over time (Figure 3). The Mount Rose population showed a significant increase in leaf quantity (mean historical = 826.7, mean contemporary = 1168.6; p = 0.0312). The other populations showed no significant change of leaf quantity (Appendix Table 3). Leaf mass per area did not show a significant change over time within any population. Overall, the contemporary samples trended towards having more leaves than the historical samples, though this difference was not significant at the p = 0.05 level.

4 Discussion

Understanding how leaf traits vary among populations is an important first step towards understanding how species respond to their environments and for understanding the degree of variation in traits across landscapes. In our study, we measured two leaf traits across multiple populations that differed in climatic conditions and how traits change across time. We found that the driest whitebark pine site, Jarbidge, had both lower leaf quantity and LMA com-

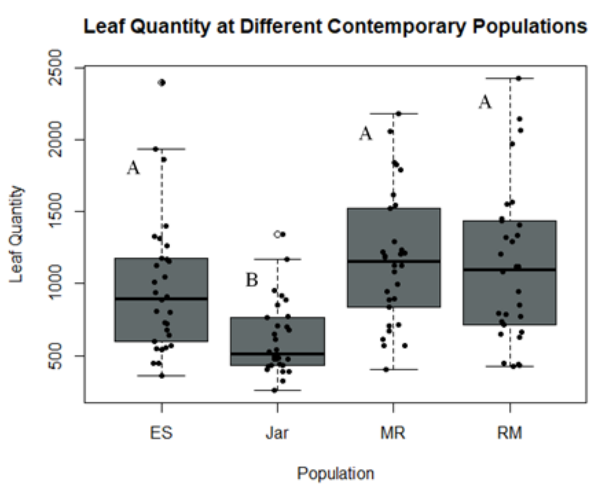

Fig. 1: Box plot of leaf quantity at four different populations (ES = Eastern Sierra, Jar = Jarbidge, MR = Mount Rose, RM = Ruby Mountain). Leaf quantity ranged from 263 to 2423 leaves per sample. Black dots represent individual data points, with two branches per tree for 30 trees per population. Solid back lines represent median values within a population. Whiskers represent 95% confidence intervals of measurements. TukeyHSD values are: ES-Jar = 0.011, ES-MR = 0.355, ES-RM = 0.581, Jar-MR < 0.001, Jar- RM < 0.001, RM-MR = 0.982.

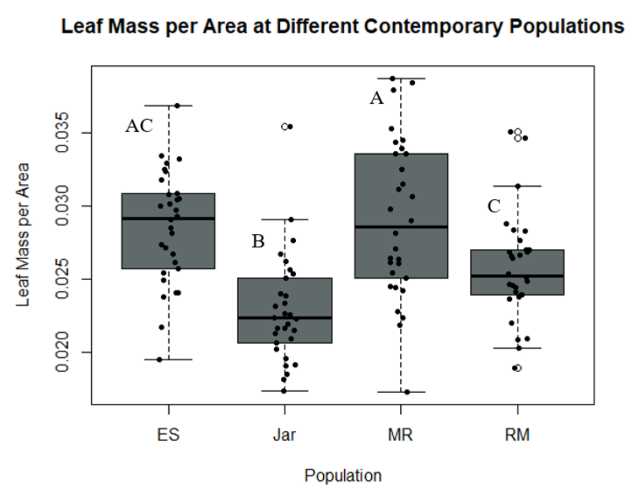

Fig. 2: Box plot of leaf mass per area at four different populations (ES = Eastern Sierra, Jar = Jarbidge, MR = Mount Rose, RM = Ruby Mountain). LMA ranged from 0.01729 (g/cm^2) to 0.03867 (g/cm^2). Black dots represent individual data points, with two leaves per tree for 30 trees per population. Solid back lines represent median values within a population. Whiskers represent 95% confidence intervals of measurements. TukeyHSD values are: ES-Jar < 0.001, ES-MR = 0.961, ES-RM = 0.055, Jar-MR < 0.001, Jar- RM = 0.049, RM-MR = 0.015.

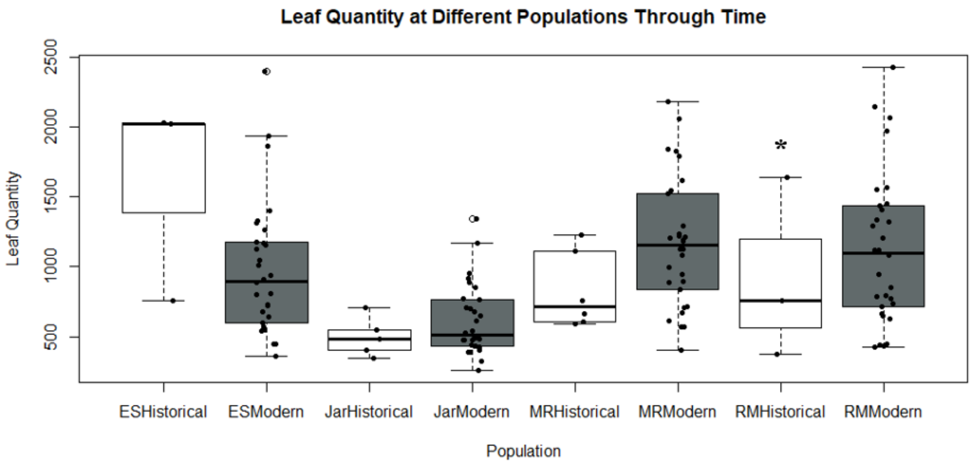

Fig. 3: Box plot showing leaf quantify for four populations (ES = Eastern Sierra, Jar = Jarbidge, MR = Mount Rose, RM = Ruby Mountain), with contemporary (Modern) and historical (Historical) values. Filled boxes represent modern populations while outlines boxes represent historical counterparts. Leaf quantity ranged from 263 to 2423 leaves per sample. Black dots represent individual data points, which, in the field, were measured for two branches from 30 trees per population. Solid back lines represent median values within a population. Whiskers represent 95% confidence intervals of measurements. P values of contemporary vs historical t-tests are as follows: ES = 0.276, Jar = 0.161, MR = 0.031, RM = 0.648.

pared to other populations. Lower leaf quantities decrease surface area for evapotranspiration, making plants more water-use efficient (*27*). However, decreased leaf mass per area has an inverse effect. Decreased LMA is associated with lower densities of mesophyll tissue within the leaves, making plants less drought-tolerant (*28*, *29*). This is of concern for Jarbidge given its notably low precipitation of the four sites and because similar LMA decreases in Scots pine were observed during drought-induced mortality (*23*).

The only population to show a change between historical and contemporary samples was Mount Rose, which showed an increase in leaf quantity over 105 years. This change in leaf quantity was not driven solely by the range of collection years within the Mount Rose population, as the exclusions of the oldest and most recent specimens yield comparable results. The exclusion of the most recent specimen does not influence the interpretation of the analysis for any of the populations. Mount Rose had the highest precipitation (Table 2) which has been increasing over time (*20*). Climate change may be driving the increasing precipitation in this area and lengthening the growing season, allowing for trees to accumulate more biomass. Increases in rainfall caused by climate change occur through the increased water holding capacity of a warming atmosphere (*30*). However, the interactions between temperature, precipitation, and plant traits are not always easily predictable (*31*). Although some interactions may extend the period for growth due to more favorable climatic conditions (*32*), climate islands may be forcing subalpine plants further up mountain tops. As trees increase in altitude there is less available land surface area, decreasing suitable habitat (*33*). The increase in leaf quantity we observed at Mount Rose may have ecological implications as it relates to leaf area index (LAI = total crown leaf area/ground area). Increased leaf quantity increases the total leaf area, which raises LAI. Increases in LAI have been shown to interact with hydrologic functioning by intercepting and sublimating snowpack (*34*). Increased canopy structure may also improve habitat for a variety of bird species (*35*), which are often used as surrogates for ecosystem diversity (*36*).

Our study indicates that there is variation in the leaf traits of contemporary populations of whitebark pine. Specifically, the number of leaves and the LMA from individuals at Jarbidge are lower than other populations. Further research is needed to understand the source of this variability, which could be due to local adaptation or genetic drift, as this population is relatively isolated and may experience limited gene flow. Additionally, the Jarbidge population has experienced high beetle mortality since 2008 (*37*), making the future of these trees uncertain. These unique differences at Jarbidge, along with the history of drought and mountain pine beetles, make this isolated population a research priority. A reciprocal transplant or common garden experiment would be able to measure the p of local adaptation within this species. Understanding how whitebark pine is changing across its range will be critical for future restoration success.

Appendix

Tab. 1: Latitude, longitude, and elevation for each tree sampled in the field. Site ID indicated population at which individual trees were sampled, 30 trees were sampled per site.

Latitude	Longitude	Elevation	Site ID	Tree #	Latitude	Longitude	Elevation	Site ID	Tree #
39.312413	119.898424	8950	Mt. Rose	1	41.857548	115.436936	7270	Jarbidge	1
39.312362	119.898861	8963	Mt. Rose	2	41.857391	115.437477	7217	Jarbidge	2
39.312364	119.898878	8963	Mt. Rose	3	41.84909	115.444765	7638	Jarbidge	3
39.312245	119.898973	8953	Mt. Rose	4	41.843518	115.447247	7348	Jarbidge	4
39.312241	119.898998	8960	Mt. Rose	5	41.843553	115.44699	7851	Jarbidge	5
39.311890	119.899682	8947	Mt. Rose	6	41.843807	115.447157	7828	Jarbidge	6
39.311401	119.900899	8940	Mt. Rose	7	41.843579	115.448263	7848	Jarbidge	7
39.311424	119.901026	8963	Mt. Rose	8	41.842507	115.449373	7904	Jarbidge	8
39.311496	119.901035	8986	Mt. Rose	9	41.842444	115.449319	7910	Jarbidge	9
39.311101	119.901286	8944	Mt. Rose	10	41.84247	115.449289	7910	Jarbidge	10
39.310912	119.901695	8924	Mt. Rose	11	41.841936	115.450639	7936	Jarbidge	11
39.310811	119.901994	8927	Mt. Rose	l2	41.839392	115.451877	8028	Jarbidge	12
39.310727	119.902797	8944	Mt. Rose	13	41.838634	115.452288	8022	Jarbidge	13
39.310803	119.903246	8953	Mt. Rose	14	41.838695	115.452261	8018	Jarbidge	14
39.310672	119.903531	8947	Mt. Rose	15	41.838948	115.452175	8018	Jarbidge	15
39.310748	119.903766	8947	Mt. Rose	16	41.839066	115.451981	8031	Jarbidge	16
39.310651	119.905277	8934	Mt. Rose	17	41.839023	115.452001	8031	Jarbidge	17
39.310640	119.905664	8944	Mt. Rose	18	41.83898	115.452047	8028	Jarbidge	18
39.309860	119.908996	8970	Mt. Rose	19	41.838892	115.451934	8038	Jarbidge	19
39.309663	119.909961	8996	Mt. Rose	20	41.838838	115.451972	8038	Jarbidge	20
39.311255	119.908486	9065	Mt. Rose	21	41.83885	115.452119	8025	Jarbidge	21
39.3116J9	119.906568	9101	Mt. Rose	22	41.838814	115.452122	8025	Jarbidge	22
39.311626	119.90626	9078	Mt. Rose	23	41.838803	115.452059	8031	Jarbidge	23
39.311842	119.906133	9114	Mt. Rose	24	41.83876	115.452175	8022	Jarbidge	24
39.311976	119.906049	9117	Mt. Rose	25	41.838678	115.452136	8031	Jarbidge	25
39.311862	119.90559	9117	Mt. Rose	26	41.838559	115.452357	8022	Jarbidge	26
39.311852	119.90518	9121	Mt. Rose	27	41.838507	115.452333	8028	Jarbidge	27
39.311820	119.904421	9052	Mt. Rose	28	41.827169	115.469279	8494	Jarbidge	28
39.311737	119.903311	9072	Mt. Rose	29	41.827161	115.469357	8497	Jarbidge	29
39.311724	119.903102	9062	Mt. Rose	30	41.827147	115.469279	850l	Jarbidge	30
38.831602	119.91452	8734	Eastern Sierra	1	40.604036	115.375705	8789	Ruby Mts.	1
38.826628	119.919865	8957	Eastern Sierra	2	40.603986	115.375550	8786	Ruby Mts.	2
38.826510	119.920294	8990	Eastern Sierra	3	40.603802	115.375453	8786	Ruby Mts.	3
38.826531	119.920453	9003	Eastern Sierra	4	40.603749	115.375594	8793	Ruby Mts.	4
38.827349	119.920184	9012	Eastern Sierra	5	40.603613	115.375658	8793	Ruby Mts.	5
38.826740	119.921615	9134	Eastern Sierra	6	40.603633	115.376040	8796	Ruby Mts.	6
38.825740	119.922309	9170	Eastern Sierra	7	40.603291	115.376535	8809	Ruby Mts.	7
38.824940	119.922564	9173	Eastern Sierra	8	40.603319	115.376415	8806	Ruby Mts.	8
38.824541	119.922449	9180	Eastern Sierra	9	40.603093	115.377345	8835	Ruby Mts.	9
38.824542	119.922601	9177	Eastern Sierra	10	40.603119	115.377317	8835	Ruby Mts.	10
38.824585	119.922675	9180	Eastern Sierra	11	40.603136	115.377194	8832	Ruby Mts.	11
38.824572	119.922664	9177	Eastern Sierra	l2	40.602721	115.376889	8822	Ruby Mts.	12
38.824547	119.922806	9180	Eastern Sierra	13	40.601179	115.378922	8917	Ruby Mts.	13
38.824628	119.922825	9180	Eastern Sierra	14	40.601186	115.378887	8914	Ruby Mts.	14
38.824545	119.922943	9177	Eastern Sierra	15	40.601084	115.378894	8930	Ruby Mts.	15
38.824300	119.922765	9190	Eastern Sierra	16	40.601127	115.378876	8930	Ruby Mts.	16
38.824302	119.922758	9190	Eastern Sierra	17	40.600981	115.378927	8930	Ruby Mts.	17
38.824226	119.923100	9186	Eastern Sierra	18	40.600939	115.378953	8930	Ruby Mts.	18
38.824293	119.923322	9177	Eastern Sierra	19	40.600844	115.379006	8934	Ruby Mts.	19
38.824399	119.923553	9180	Eastern Sierra	20	40.600856	115.379040	8934	Ruby Mts.	20
38.823995	119.922455	9213	Eastern Sierra	21	40.600824	115.379235	8947	Ruby Mts.	21
38.824104	119.922350	9206	Eastern Sierra	22	40.601015	115.379292	8944	Ruby Mts.	22
38.824007	119.922147	9219	Eastern Sierra	23	40.60111	115.379351	8944	Ruby Mts.	23
38.824016	119.922048	9232	Eastern Sierra	24	40.601083	115.379739	8957	Ruby Mts.	24
38.823538	119.922776	9216	Eastern Sierra	25	40.601074	115.379809	8960	Ruby Mts.	25
38.823023	119.922743	9232	Eastern Sierra	26	40.601046	115.379880	8963	Ruby Mts.	26
38.822823	119.923006	9232	Eastern Sierra	27	40.601014	115.379955	8973	Ruby Mts.	27
38.822874	119.923051	9229	Eastern Sierra	28	40.600821	115.379924	8973	Ruby Mts.	28
38.822957	119.923152	9222	Eastern Sierra	29	40.600792	115.379943	8973	Ruby Mts.	29
38.822817	119.923563	9226	Eastern Sierra	30	40.600668	115.379951	8976	Ruby Mts.	30

Tab. 2: List of herbarium specimens used from the University of Nevada, Reno herbarium. Four populations were available for sampling (ES = Eastern Sierra, Jar = Jarbidge, MR = Mount Rose, RM = Ruby Mountains). Year collected is based on date present on herbarium sheet. Each sheet has a distinct herbarium code listed below. Specimen 11525 was unable to have LMA data collected because of concern of damaging the specimen.

Population	Year Collected	Herbarium Code
ES	1949	11525*
ES	1980	11533
ES	1996	78023
Jar	1996	24553
Jar	1996	24555
Jar	1994	24560
Jar	1994	24565
Jar	1994	24569
MR	1967	11523
MR	1912	11524
MR	1946	11536
MR	1940	11539
MR	1939	24552
MR	1938	78027
RM	1962	11538
RM	1995	24551
RM	2006	24559

Tab. 3: Average leaf quantity and LMA (g/cm^2), for both each contemporary and historical population.

Population	Avg. Leaf Quantity	Avg. LMA (g/cm^2)
Jar	616	0.0229
Jar-Historic	498	0.0237
RM	1125	0.0257
RM-Historic	923	0.0286
MR	1168	0.0287
MR-Historic	827	0.0295
ES	979	0.0285
ES-Historic	1601	0.0285

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