***Agave palmeri* restoration: salvage and transplantation of population structure**

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Abstract

Agave palmeri (Palmer's agave) is a long-lived, monocarpic, perennial succulent which provides a critical flower nectar food source for the threatened species, *Leptonycteris curasoae* (lesser long-nosed bat) among other animals. *Agave palmeri* flower only once after approximately 25 years. To support the demography needed to have some plants flowering every year, wild populations of *A. palmeri* must be conserved and mining, construction, and recreational impacts must be mitigated. Collecting, storing, and transplanting wild plants was tested as a potential method for restoring and maintaining *A. palmeri* populations. In January 2009, 387 wild plants were collected, roughly half the plants were potted in field soil, and the remainder were placed in pots without soil (bare-root) and covered with burlap cloth. During 6-months storage, 1% of plants potted in field soil died while 31% of bare-root plants died. In July 2009, a denuded and scarified field plot was planted with the surviving 277 *A. palmeri* individuals. Plants received one of three water treatments: a 90-day slow-release gel irrigation supplement, 8 L (2 gal) of water, or no water or gel. Three years after transplanting, survivorship was assessed. The watering treatments had no significant effect on survivorship. The number of green leaves at the time of collection was the most important factor in predicting if the plants lived, died, or survived to flower before dying . Mortality is concentrated in the smallest and largest plants. Transplanting appears to be a viable method of returning diverse size classes of *A. palmeri* to disturbed sites.

Keywords: semi-arid lands, Arizona, land reclamation, *Leptonycteris curasoae,* Palmer's Agave.

Introduction

Agave palmeri Engelm. (Palmer's Agave) is an interesting, regionally common, and attractive plant species. In addition to its contribution to native biodiversity, a main motivation for *A. palmeri* conservation is that their flower nectar provides a critical food resource for the threatened bat species, *Leptonycteris curasoae* Miller (Lesser Long-Nosed Bat; Ober and Steidl 2004; Ober et al. 2005). In turn, pollination by *L. curasoae* may be critical in maintaining the stability and longevity of future *A. palmeri* populations (Schaffer and Schaffer 1977; Howell and Roth 1981; but see Slauson 2000) so bat conservation may also be *A. palmeri* conservation. Individual *A. palmeri* probably grow for 20 to 30 years before flowering in late spring through early autumn (J. Fehmi *pers. obs.*). *Agave palmeri* are monocarpic and die after flowering. This long maturation period and single flowering episode make *A. palmeri* especially susceptible to the increasingly common human disturbances in its range across southeastern Arizona, southwestern New Mexico, USA, and the adjacent regions of northern Sonora and Chihuahua, Mexico (Fig 1).

While many plant species can be restored from seed after disturbance, this does not work well for *A. palmeri*. A seed-based restoration effort would result in an even-aged cohort which over a large area would not support bats for as much as 30 years afterward. Another issue is that *A. palmeri* seeds show little or no germination in bare soil (Pavliscak et al. 2015) and would most likely require a secondary round of seeding after other plants have established. Even with cover from established plants, low germination in restoration conditions seems likely compounded by high mortality because young agave plants are more vulnerable to environmental extremes and herbivory than adults (Turner et al. 1966; Jordan and Nobel 1979). Research by Nobel (1977) estimated that only 1 in 1.2 million seedlings of *A. deserti* Engelm. survive to adulthood albeit in a species with a generally asexual (clonal) reproductive strategy. Gentry (1982) attributed similar survival estimates to representatives of the genus but it is unknown how well this is reflected in a species like *A. palmeri* with a generally sexual (seed-based) reproductive strategy. These seed and small-plant mortality issues add greatly to the resources required to establish *A. palmeri* and hinder the establishment of a multi-age population demography that could sustain bat populations with successive years of flowering.

Salvaging *A. palmeri* from impact zones and transplanting them outside of disturbed areas, or back into disturbed areas undergoing restoration, have been common strategies. As long as the salvaged *A. palmeri* survive and represent a range of ages with the corresponding range of flowering, this strategy seems likely to support bat populations as well as provide the on-going seed source needed to establish viable *A. palmeri* populations. However, little is known about the outcome of *A. palmeri* transplants, thus limiting understanding of the implications of large-scale restoration plans.

In order to assess the response of *A. palmeri* to transplanting in southern Arizona, we assessed conditions and attributes at the time of collection, storage practices, and application of water at the time of transplanting. This documented the response of *A. palmeri* to a suite of environmental variables that would likely be confronted in a large-scale transplantation effort. Choice of individuals to collect, method of storage, and water availability post-transplant are all treatments that managers must explicitly decide when designing a restoration strategy involving this species.

Materials and Methods

Experimental site

The study site was in the rolling foothills of the southern Arizona USA (31°50’36”N, 110°45’00”W, Fig. 1). The local vegetation is oak woodland and grama grassland with abundant *Quercus emoryi* Torr., *Q. arizonica* Sarg., *Juniperus deppeana* Steud., *Mimosa aculeaticarpa* Ortega var. *biuncifera* (Benth.) Barneby, *Nolina microcarpa* S. Watson, and *Bouteloua curtipendula* (Michx.) Torr. Slopes face dominantly east, southeast, and northeast. The shallow well-drained calcareous soils are classified as in the Mabray-Chiricahua Rock association, and are developed from conglomerates, mudstones, sandstones, and rock outcrops (NRCS 2010). Mabray soils are Loamy-skeletal, carbonatic, thermic Lithic Ustic Torriorthents and Chiricahua soils are Clayey, mixed, superactive, thermic, shallow Ustic Haplargids (NRCS 2010). Local records indicate an annual average of 43 cm (17 in) of rainfall per year with more than half falling in the summer monsoon season (July-September) and the remainder falling in the winter, occasionally as snow (Tetra Tech 2009). Annual air temperatures generally range from -4-30°C (25-85°F) with over 100 days of frost (USDA 2006).

Agave Collection

In the winter of 2009, five 4000 m^2 (13,000 ft^2) collection blocks with dense populations of *A. palmeri* were identified on private land slated for building construction (centered at approximately 31°50'34.8"N, 110°44'59.5"W) on the northeastern side of the Santa Rita Mountains. Each block had similar vegetation and elevation [1550-1600 m (5100-5250 ft)] and were within 3 km (2 mi) of each other. Similar to most succulents, *A. palmeri* are shallow rooted (McDaniel 1985) but the largest rosettes were approximately 1.2 by 1.2 m and weighted an estimated 60 kg plus the weight of the soil if that were collected with the roots. Approximately 90% of *A. palmeri* were excavated using a backhoe and the remainder were excavated by hand. This resulted in limited representation of areas isolated by steep drainages or dense tree-dominated vegetation where access was limited but likely represents real-world salvage practices. *Agave palmeri* were collected 6-12 Jan 2009 in two stages: first for the transplant methods experiment and then for the bare root storage observations. Each *A. palmeri* had their original southern exposure marked and was tagged for transport consistent with state laws.

For the transplant methods experiment, five size classes were determined based on the number of leaf whorls. Whorls (classes 1-5) were measured by laying a straight-edge across the center of each plant, and counting the number of sequential leaves radiating from the central spike, so that one leaf whorl was labeled size class 1, two whorls, size class 2, etc. (Howell 1995). Approximately 10-15 individuals from each size class were selected in each block, resulting in 45 plants per size class except for size class 5. Locating plants large enough to be classified size class 5 (the largest category in the experiment), but small enough to be potted, transported, stored, and replanted in the same method as the other plants in the study was challenging, resulting in collection of only 19 of this size category. A minimum of 10 m (33 ft) between individuals to be collected was maintained in order to minimize the possibility of collecting genetic clones.

Because *A. palmeri* often grows in loose colonies (Gentry 1982) with some adjacent plants potentially occurring from clonal offsets and others being recruited from seed, it was not uncommon for plants neighboring the target individual to be unearthed. These individuals were also collected and became the bare-root treatment specimens. They were tapped free of soil among their roots and deposited into nursery pots without soil. Although these plants are potentially related to the target individuals by seed or cloning, and the post hoc design is far less than ideal, the resulting data allows analysis of a range of methods from most resource intensive (potted in soil) to least resource intensive (bare root).

In total, 199 plants were collected for the soil treatment and another 188 plants were collected for the bare-root treatment. Location, plant height and width, slope aspect and inclination, proximity to neighboring agave plants, canopy cover by other plants, surface cover (gravel, cobble, soil, and organic matter), and dominant vegetation were documented for each plant.

Storage

Agave palmeri potted in soil and bare-root treatment plants were transported to the University of Arizona Campus Agricultural Center (32°16'48.9"N, 110°56'29.8"W) in Tucson, Arizona, and stored from 6 Jan-14 Jul 2009 in a greenhouse with the ceiling and wall panels removed and replaced with shade cloth. A shade house was used in this experiment because it better matched the likely real-world practices than a climatecontrolled facility (e.g. Bainbridge 2007). Plants potted in soil were watered to field capacity once per month until temperatures warmed in April, at which time they were watered every 2 weeks (Irish and Irish 2000). Bare-root plants remained in empty pots and entire plants (roots and shoots) were covered with 2 sheets of burlap cloth that was moistened every two weeks.

Transplanting

In the summer of 2009, a 2400 m^2 (0.6 acre) transplanting plot was prepared on a moderate (12°) east-facing slope (31°50'49" N, 110°44'58" W). Vegetation was removed with a bulldozer, and the soil surface was raked with a ripper to a depth of 15-30 cm (6-12 in) to simulate soil conditions after disturbance. Transporting and planting occurred from 12-17 Jul 2009, in an effort to coincide with the summer monsoon rains. A 46 cm (18 in) auger on a skid steer drilled 64 cm (25 in) deep holes at each planting location. Individual plants, treatments, and planting locations were completely randomized, although due to different numbers of size classes, there were uneven numbers of treatments and replications within and between sites, resulting in an unbalanced randomized block design with notably fewer size class 5 (the largest category in the experiment). Additionally, because the bare root plants had a high mortality rate in storage, there were fewer plants of this treatment than of the soil treatment.

During transplanting, plants were oriented so that their original southern exposure again was facing south in order to minimize the uneven application of stress between plants from unaccustomed sun exposure (Irish and Irish 2000). Care was taken to settle the base of each plant to ground level so that planting depth and method were standardized. Three watering treatments were used: a 90-day time-release gel pack (model DWP-TG, DriWater, Santa Rosa, CA) buried with gel directly against the root ball on the south side of the agave, 8 L (2 gal) of water slowly applied directly over the rosette for maximum local infiltration and minimal run-off, and a treatment with no supplemental water or gel. A Taylor 2710N rain gauge (Taylor Precision Products, Oak Brook, IL) was installed in the center of each of the three sites, and was manually checked on a monthly basis. A post-transplant inventory was conducted in mid-August 2012 – three years after transplanting.

Analysis

The mortality data from the designed part of the study, the agaves potted in soil, was analyzed using a chi-square test. Recursive partitioning was used to analyze the remaining data (R package "rpart"; Therneau et al. 2015). To avoid over-fitting the data, variables for inclusion in the final model were selected as the group that minimized the cross-validated error. To ensure that the variables selected were not an artifact of their order, a random forest procedure (R package "randomForest"; Liaw and Wiener, 2002) was used to iteratively test the possible combinations of three variables (as described in Strobl et al. 2009). The resulting ranks and magnitudes of the importance analysis should match the recursive partitioning analysis (Williams 2011). Only 247 individuals with complete information from all data fields and that were alive to be transplanted were included in the recursive partitioning and random forest analysis. All statistics were done in R (R Core Team, 2019).

Results

Temperatures recorded between Jul 2009-Apr 2010 at a weather station within 5 km (3 mi) from the transplanting plot showed a monthly mean range between 6.6-25.2°C (43.9-77.4°F; Table 1). Prior to replanting on 14 Jul 2009, the site had received 48 mm (1.9 in) of precipitation. Including July rainfall prior to replanting, this is between 18-37% below the long-term average seasonal precipitation for the area of 230-300 mm (9-12 in; Sellers 1978).

Mortality in storage

While in storage, 96% of *A. palmeri* plants potted in soil were generally in good condition, with few dead leaves, and minimal leaf discoloration, thinness, or wrinkling. Only two plants died (a 1% mortality rate): one a size class 5 that flowered and the other a size class 1 that produced an offset (clonal ramet). In contrast, during this time only 4% of bare-root plants were in visibly good condition. Additionally, 31% of bare-root plants died while in storage, the majority of which were small (75% size class 1, 22% size class 2, 3% size class 3). In total, 45% of all the size-class-1 plants collected for the bare-root treatment died while in storage, in addition to 28% of all size-class-2 and 7% of all size-class-3 plants.

Field mortality in the designed experiment

For the designed experiment (the *A. palmeri* which were previously potted in soil), the overall mortality rate was 17% three years after *A. palmeri* were transplanted into the field site. There were no significant (p = 0.27) differences among the gel-pack, watering, or dry planting treatment of the transplants nor among the size classes (Table 2).

All variable analysis of transplants:

The main factor predicting the fate of the *A. palmeri* three years after transplanting was the number of green leaves as determined by the cross-validation error as well as the importance analysis (Table 3). The accuracy measure (Type 1 error reduction) indicated *A. palmeri* green leaf count and potted vs bare root were the most important factors. The Gini measure (Type 2 error reduction) similarly indicated *A. palmeri* green leaf count but not potted vs bare root. Transplanted *A. palmeri* with between 8 and 40 green leaves at the time of field collection, faired the best with a 14.8% mortality rate (Fig. 2). For plants with 7 or fewer leaves, nearly half (45%) died. For *A. palmeri* with more than 40 leaves, 57% flowered and died. Adding the Potted vs. Bare root treatment would have only slightly improved the classification of agaves with between 4 and 7 green leaves which was of marginal benefit and not included.

Discussion

This experiment investigated the response of wild *A. palmeri* plants in a transplantation effort involving salvaging, storing for 6 months, and replanting in a disturbed area. Overall, results from the three-year monitoring period suggest that *A. palmeri* responded well to transplanting.

Storage treatment

While bare root plants were associated with significant mortality (31%) while in storage, they were not different from the plants potted with soil after being transplanted onto the study plot. The relatively high survival in storage and positive response once transplanted appears to show a drought adaptation enabling substantial root drying. *Agave palmeri* roots have been thought to normally lose soil contact because, as drying increases, both soil and roots lose volume which can create an air gap between the soil and roots similar to that described by Nobel and Cui (1991). As succulents, agave store water in their leaves and in the base of the rosette which is exported to the roots to keep them alive when there is a lack of soil moisture (North and Nobel 1998). The higher survival of the larger plants seems attributable to large plants being able to store more water per unit surface area, thus able to tolerate longer droughts with up to 95% plant water loss before irreversible cellular damage, as described by Nobel (1988, 1994).

Agave palmeri potted in soil for storage had only a 1% mortality rate. These plants were watered to field capacity once a month from January-April, and then bimonthly through late spring until replanting. The irrigation strategy was intended to provide the basic water required to keep plants alive, but in retrospect, the amount and frequency of irrigation was likely ample water to facilitate growth in this drought-adapted species. Thus, by the July planting period, these soil treatment plants had already been growing for some time, likely since warmer weather began in April.

Water and size class treatment

The supplemental water and gel-pack treatments in this experiment were selected with the intention of minimizing time and logistics required for implementation. The ability of other agave species to rapidly respond to a pulse of water with new root growth and immediate water uptake (Nobel and Cui 1991; Nobel 1988; North and Nobel 1998), suggested that water availability, even on a single occasion, could have a dramatic impact on the survivorship and growth of transplants.

Contrary to expectations, neither the supplemental water nor adding a gel-pack reduced *A. palmeri* mortality across both potted and the bare-root transplants. A possible explanation for this lack of response is that replanting occurred at the beginning of the summer monsoon rainy period. Although rainfall was below the long-term average at the time of replanting, 140 mm (5.5 in) fell on the study plot that season, half of which occurred within a month after planting. This rainfall may have overridden the effect of water treatments, suggesting that supplemental irrigation may not be critical for plant survivorship when transplanting coincides with periods of sufficient precipitation. If planting had occurred during a more climatically unfavorable period, for example before the warm temperatures and dry weather of the spring season, the application of these water treatments may have had a more important role in influencing mortality and growth.

The size of the plant at the time of collection was the most important factor predicting its survival through the next three and a half years. This was especially apparent for small plants where nearly half of the *A. palmeri* having fewer than 8 green leaves died after transplanting. While little research has been done on *A. palmeri*, younger plants of other agave species with similar smaller volume to surface ratios and less developed root systems have been shown to be more sensitive to extremes in temperature and moisture availability (Jordan and Nobel 1979; Nobel 1988). Young plants of other agave species have been shown to benefit from a nurse plant or rock to provide protection from unfavorable environmental variation (Jordan and Nobel 1979; Gentry 1982; Arizaga and Ezcurra 2002; Rangel-Landa et al. 2015). The open plot where transplanting occurred in our experiment did not offer any such protection to young plants but was thought to represent the typical conditions where salvage agave would be transplanted.

There were no changes in mortality attributable to the five plant-size classes which we used to ensure balanced representation of relative age groups in the designed experiment. Given that size was a main factor associated with mortality, the ad hoc assignment of five size classes appeared to have missed the important break points in the plant response as well as combined older plants from poor soil with younger plants from more productive soils. The number of leaves has been used as a non-destructive indicator of agave productivity (Nobel 1984, 1988; Quero and Nobel 1987), and in our study, number of leaves was a better variable to estimate mortality risk for *A. palmeri*.

Recommendations

Re-establishing *A. palmeri* in areas of large-scale disturbance will most likely involve transplanting. Seeds seem unlikely to establish (Pavliscak et al. 2015) and if they did, young plants likely have high mortality rates (Gentry 1972; Nobel 1977; Jordan and Nobel 1979). Even if seeding were effective, it would not resolve issues related to *A. palmeri* use as a bat food resource because seeding would result in an even aged cohort with an approximate 25-year lag in flower production. Transplanting of variously-aged *A. palmeri* plants may be essential to an effective restoration strategy in this setting.

The primary variable of interest in this study is the long-term reproductive success of transplants to provide relatively consistent inter-annual nectar resources to support for *L. curasoae*. Having plants flower within three years of transplanting may support these goals but given the life span of the species (≤ 25 years) limiting the number of large plants to 10% of those collected may be warranted. Including some large plants seem advisable because after flowering they will contribute seeds to resume the *A. palmeri* population cycle. The benefit for bat foraging is also limited with the collection of the smaller *A. palmeri* given that they die at higher rates. If the collection effort is relatively equal among plants despite their size differences, then the majority of effort should be concentrated on plants with between 8 and 40 leaves. If smaller plants are collected, they may benefit from longer storage potted in soil to allow them to gain size or they may benefit from transplanting practices tailored specifically to them. More research is needed.

The survival of almost 70% of the bare-root stored plants offers the opportunity for a bet hedging strategy for agave collection when time or funds are limited. Plants can be stored in soil (pots or temporarily transplanted) up to some maximum and the remainder kept as bare-root plants. This may allow for a much larger effort with a predictable minimum level of survival in storage.

Acknowledgements: This study was carried out with financial support from Rosemont Copper. J.S.F. received partial support from the University of Arizona Agricultural Experiment Station.

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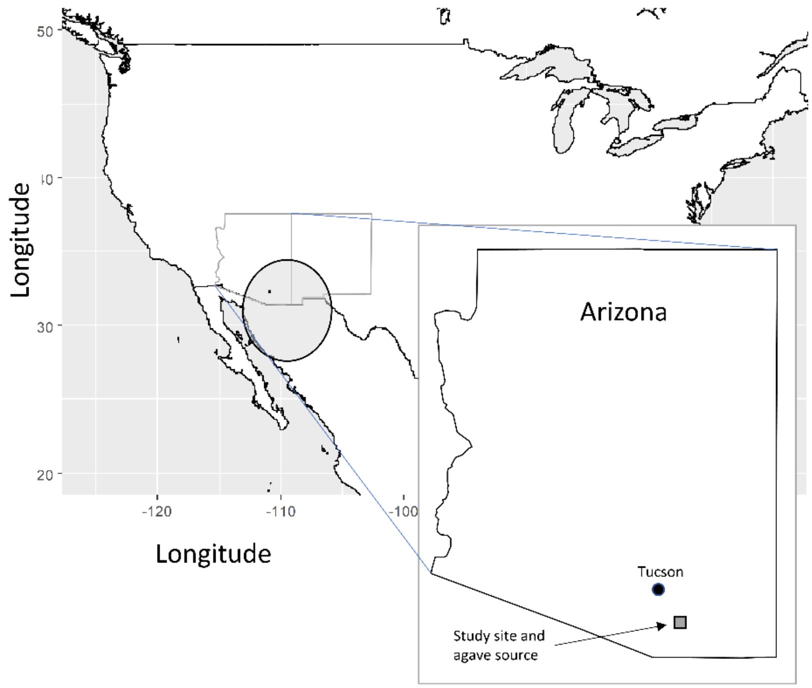

Figure 1. Regional map showing the general study site and *Agave palmeri* source location (indicated box) and geographic range of distribution of *A. palmeri* (gray circle based on SEInet (2020) data).

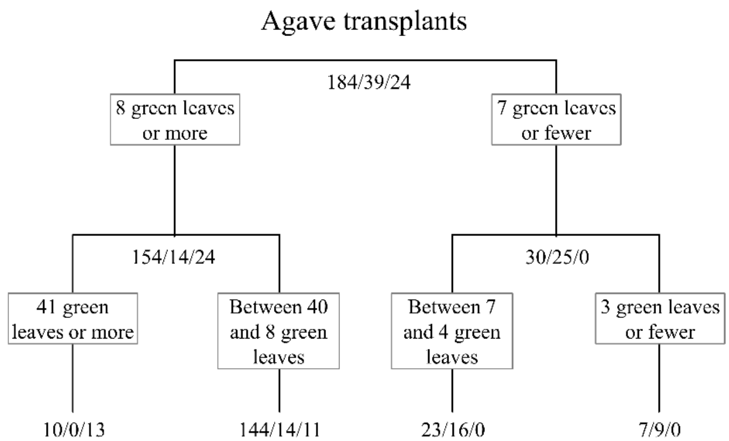

Figure 2. Recursive partitioning analysis of 247 *Agave palmeri* transplants. Order of responses is Lived/ Died without flowering/ Flowered and died. For all transplants 184 plants lived/ 39 died without flowering/ 24 died after flowering. The highest percentage of plants that survived had between 8 and 40 green leaves at the time of field collection.

Table 1. Mean temperatures and total precipitation (averaged between sites) from 14 Jul 2009-14 Apr 2010, at the study plot in the northeast Santa Rita Mountains, Pima County, Arizona.

SEASON	**Mean temperature (C)**			**Total precipitation**
	Min	**Max**	**Ave**	**(mm)**
Summer (Jul-Sep)	19.2	28.8	24.1	140
Fall (Oct-Nov)	9.8	19.8	14.7	0
Winter (Dec-Feb)	2.5	11.4	6.8	129
Spring (Mar-Apr)	6.1	16.6	11.6	96
AVERAGE	9.7	19.3	14.6	365 Total

Table 2. Three-year field mortality of transplanted *A. palmeri* that had been previously stored in pots with soil for six months. The fractions shown are the number that died as the numerator and the total number in that treatment and size class combination as the denominator. Classes 1-5 were determined by laying a straight-edge across the center of each *A. palmeri* plant, and counting the number of sequential leaves radiating from the central spike, so that one leaf whorl was labeled size class 1, two whorls, size class 2, etc. The three watering treatments were: no supplemental water or gel (Dry), a 90-day time-release gel pack buried against the root ball (Gel), 8 L of supplemental water applied immediately after transplanting (Water).

		Treatment		
		Dry	**Gel**	**Water**
Size Class	**1**	3/15	1/15	1/15
	2	0/15	2/15	3/15
	3	0/15	1/15	3/15
	4	3/15	7/15	3/15
	5	2/6	3/6	2/6

Table 3. Relative influence (Importance) of predictive factors from the permutation of factor combinations (Random Forest Analysis)

Factor	Mean Decrease Accuracy (Type 1 Error Reduction)	Mean Decrease Gini (Type 2 Error Reduction)
Agave green leaf count	21.298	23.871
Potted vs Bare root	17.991	7.047
Bare soil (%)	5.883	8.345
Adjacent grass presence	4.945	1.528
Adjacent woody species presence	4.288	3.947
Adjacent canopy cover (%)	4.156	7.406
Slope (%)	3.377	9.826
Adjacent succulent presence	3.356	2.052
Organic matter (%)	2.539	6.915
Elevation (m)	1.539	9.421
Aspect	1.224	8.509
Treatment (Watered, Dry, or Gel pack)	-0.366	4.365
Block	-1.494	3.570
Distance to nearest Agave	-2.428	2.638