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Abstract

The nurse plant phenomenon is an important form of facilitative interaction where a “nurse-plant” provides shelter from abiotic or biotic stress to a “beneficiary” plant. Plant facilitation strongly depends on nurse-plant traits such as size or age. This effect has been mostly attributed to the amelioration of abiotic conditions under larger nurse-plants. However, the effect of nurse-plant size on the overall facilitative process (quantitative and qualitative components) remains largely unexplored, particularly for increasing levels of biotic stress. Here, we investigated the effect of nurse-plant size on the quantitative (recruitment density) and qualitative (recruit shape and growth) components of plant facilitation along two contrasting herbivore-stressed environments. We measured natural oak recruits located under and outside nurse-plants of different size and age. Results show that both components of plant facilitation increased with nurse-plant size but were more pronounced at high biotic stress. Quantitatively, at high biotic stress, facilitation occurred in nurse plants of approximately half the size of those subject to low biotic stress. Interestingly, the qualitative component revealed different results depending on the ontogenetic stage of recruits, with a significant effect of nurse-plant size on large recruits (saplings) but not on small recruits (seedlings). Additionally, at higher biotic stress, more beneficiaries were found further inside the nurse-plant. Similarly, oak recruits located further inside the nurse plant showed greater plant quality. Although nurse-plant age and size were highly correlated, the spatial distribution and quality gradient of recruits suggests that nurse-plant size rather than age enhances plant facilitation in herbivore-dominated environments. We conclude that nurse-plant size plays a crucial role in plant facilitation but its net facilitative effect is strongly mediated by the level of biotic stress and the ontogeny of beneficiaries. We highlight the importance of considering both components (quantity and quality) of plant facilitation to fully understand how plant-plant interactions change at increasing levels of stress.

Keywords	Mediterranean environments; herbivory; plant ontogeny; nurse-plant age; stress gradient hypothesis; wild ungulates.
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Highlights:

- Quantity and quality of oak recruits improved with increasing nurse-plant size
- Overall facilitation was mediated by the biotic stress and ontogeny of recruits
- Under high biotic stress, facilitation occurred at smaller nurse plant sizes
- Nurse plant size had a positive effect on quality of saplings but not on seedlings
- Sapling quality improved with increasing distance to the nurse-plant edge

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Nurse plant size and biotic stress determine quantity and quality of plant facilitation in oak savannas

Running head

Nurse plant size and biotic stress determine plant facilitation

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ABSTRACT

The nurse plant phenomenon is an important form of facilitative interaction where a “nurse-plant” provides shelter from abiotic or biotic stress to a “beneficiary” plant. However, plant facilitation strongly depends on nurse-plant traits such as size or age. This effect has been mostly attributed to the amelioration of abiotic conditions under larger nurse-plants. However, the effect of nurse-plant size on the overall facilitative process (quantitative and qualitative components) remains largely unexplored, particularly for increasing levels of biotic stress. Here, we investigated the effect of nurse-plant size on the quantitative (recruitment density) and qualitative (recruit shape and growth) components of plant facilitation along two contrasting herbivore-stressed environments. We measured natural oak recruits located under and outside nurse-plants of different size and age.

Results show that both components of plant facilitation increased with nurse-plant size but were more pronounced at high biotic stress. Quantitatively, at high biotic stress, facilitation occurred in nurse plants of approximately half the size of those subject to low biotic stress. Interestingly, the qualitative component revealed different results depending on the ontogenetic stage of recruits, with a significant effect of nurse-plant size on large recruits (saplings) but not on small recruits (seedlings). Additionally, at higher biotic stress, more beneficiaries were found further inside the nurse-plant. Similarly, oak recruits located further inside the nurse plant showed greater plant quality. Although nurse-plant age and size were highly correlated, the spatial distribution and quality gradient of recruits suggests that nurse-plant size rather than age enhances plant facilitation in herbivore-dominated environments.

We conclude that nurse-plant size plays a crucial role in plant facilitation but its net facilitative effect is strongly mediated by the level of biotic stress and the ontogeny of beneficiaries. We highlight the importance of considering both components (quantity and quality) of plant facilitation to fully understand how plant-plant interactions change at increasing levels of stress.

Keywords: Mediterranean environments, herbivory, plant ontogeny, nurse-plant age, stress gradient hypothesis, wild ungulates.

INTRODUCTION

Positive interactions among plant species are common in a wide range of ecological settings (Callaway, 1992; Bertness & Leonard, 1997; Tirado & Pugnaire, 2005; Soliveres et al., 2011). An important form of facilitative interactions is the nurse plant phenomenon, where some plants (the "nurse") facilitate germination, establishment and development of other plant species (the "beneficiary") by providing shelter from abiotic stress, protection against biotic consumption, or both (Franco & Nobel, 1988; Valiente-Banuet & Ezcurra, 1991; Brooker et al., 2008; Gómez-Aparicio et al., 2008; Leiva et al., 2015).

The stress gradient hypothesis (SGH) predicts that the frequency of facilitation directly increases with stress intensity (Bertness & Callaway, 1994; Callaway, 2007). Therefore, in stressful environments, beneficiary species are often more dependent on nurse plants than in more benign environments (Pugnaire et al., 1996a; Smit et al., 2008; Maestre et al., 2009; Smit et al., 2009). For example, in arid and semi-arid environments, pioneering shrubs progressively change the environment underneath them as they increase in size and age, facilitating the establishment of less stress-tolerant species (Pugnaire et al., 1996b). Indeed, nurse-plant size influences the balance of facilitative and competitive effects, with larger nurse plants supporting greater beneficiary richness and biomass in both xeric and mesic sites (Tewksbury & Lloyd, 2001). These studies suggest that the main cause of the increased facilitative effect of larger nurse plants was the ameliorated abiotic conditions under them (Pugnaire et al., 1996b; Tewksbury & Lloyd, 2001; Domínguez et al., 2015). Similarly, in herbivore-dominated environments, large nurse plants may also provide better conditions against biotic stress (e.g. large herbivore stress) constituting a physical barrier against browsing (Perea & Gil, 2014a). In this regard, the larger the plant size, the higher the probability of the beneficiary to be separated from the nurse-plant edge where the risk of being browsed is higher. Interestingly, in environments dominated by biotic stress (herbivore pressure), facilitation mostly occurs through unpalatable nurse plants of sufficient size to prevent consumption of the beneficiaries (Hay, 1986; Callaway et al., 2005; Smit et al., 2006; Perea & Gil, 2014a; Perea et al., 2016). Furthermore, in extreme conditions, biotic stress by herbivores can significantly modify the sign (e.g. from competitive to facilitative) and strength of plant-plant interactions (Callaway et al., 2005; Baraza et al., 2006; Smit et al., 2009; Perea & Gil, 2014a). As large herbivore populations, particularly wild ungulates, have increased over the last decades, browsing damage has imposed a limit on tree recruitment in open environments (Côté et al. 2004; Gordon et al., 2004). Therefore, understanding the effect of nurse plant size and age at contrasting levels of herbivory is of high ecological importance and deserves further research (Smit et al., 2007; Gómez-Aparicio et al., 2008; Perea & Gil, 2014b).

Plant facilitation can be evaluated by quantitative and qualitative components, similar to other biotic interactions (*sensu* Schupp et al., 2010). The quantitative component of plant facilitation refers to the number of recruits successfully established under the nurse plant, whereas the qualitative component refers to the performance and growth once plants have established. Most studies have focused on either qualitative or quantitative facilitation but have very rarely incorporated both (see Maestre et al., 2005). As stress conditions may change across different recruit ontogenetic stages (Armas & Pugnaire 2009), results on the qualitative and quantitative components of plant facilitation may vary over time. Furthermore, nurse-plant size may also affect quantitative and qualitative components of plant facilitation differently as larger plants create greater shelter that increases recruit density (Pugnaire et al., 1996b; Tewksbury & Lloyd, 2001), but favors stronger competition with the underneath beneficiaries (Schwinning & Weiner, 1998; Valladares & Pearcy, 2002). Similarly, beneficiary plants located further inside the nurse plant (i.e. at farther distances from the nurse-plant edge) will benefit from greater protection from both, abiotic and biotic stress, and are therefore expected to receive stronger facilitative effects under larger nurse plants. However, to the best of our knowledge, no study has fully evaluated the effect of nurse-plant size on the magnitude (quantity and quality components) of the facilitative process at contrasting levels of biotic stress.

In this study we aimed to investigate the effect of nurse-plant size on the quantitative (recruitment density) and qualitative (recruit shape and growth) components of plant facilitation along two contrasting herbivore-dominated environments, with high and low densities of wild ungulates. We specifically focused on the facilitative relationship between a well-known nurse shrub (*Baccharis pilularis* DC) and the beneficiary coast live oak (*Quercus agrifolia* Neé), which strongly depends upon *Baccharis* cover to regenerate in California oak savannas (Callaway & Davis, 1998; Zavaleta & Kettley, 2006; Perea et al., 2017). We hypothesize that both quantitative and qualitative components of plant facilitation will increase with nurse-plant size but will be strongly mediated by biotic stress (herbivore pressure). Specifically, we tested the following predictions: (1) overall plant facilitation (both quantity and quality) will increase at higher levels of biotic stress (herbivore stress) following the SGH framework, (2) nurse plants will facilitate greater density of recruits with increasing plant size; (3) the qualitative component of plant facilitation will also increase with both nurse-plant size and distance to the nurse-plant edge; and (4) facilitative effects due to increasing nurse-plant size will be proportionally greater at higher biotic stress.

MATERIALS AND METHODS

Study sites

We selected two nearby sites (distance < 3 km; Fig. 1) located in the interior foothills of Northern California (USA) based on their different level of biotic (herbivore) stress: a) Jasper Ridge Biological Preserve, with high deer abundance and, hence, high herbivore stress (hereafter, HHS) and b) the Stanford University Dish Area, with comparatively lower herbivore stress (hereafter, LHS). Previous estimations showed 5.4-fold greater deer abundance in HHS than in LHS (Perea et al., 2017).

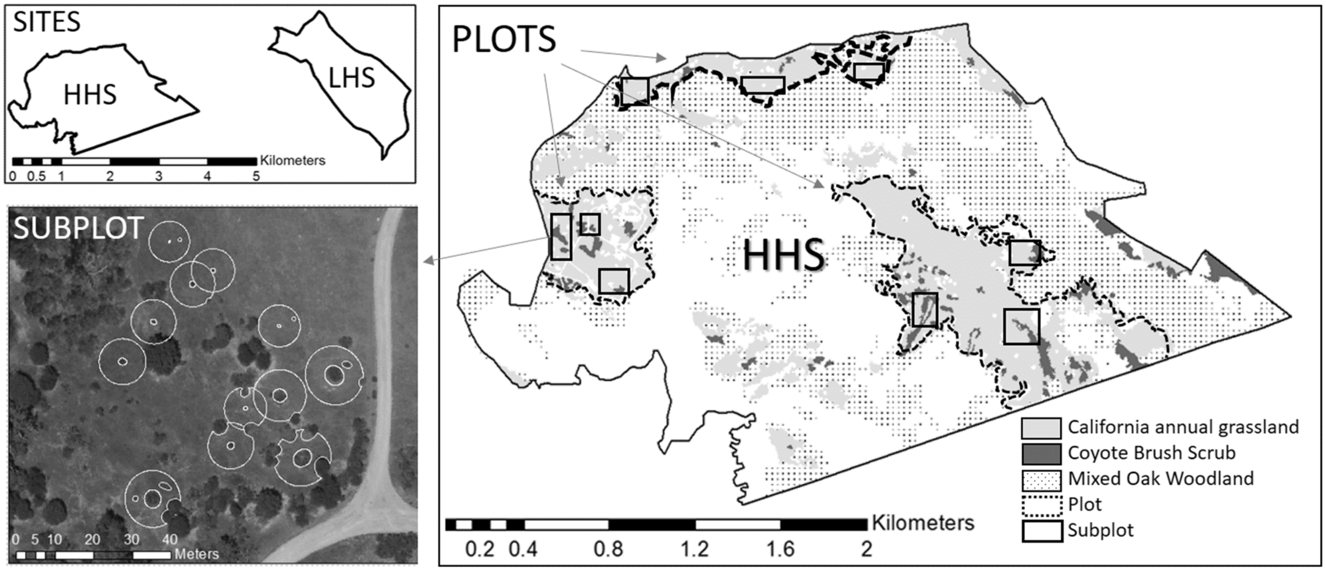

Fig. 1. Sampling design with Plots and Subplots nested within the fixed factor Site. Each site (HHS and LHS) contained three large grassland areas (Plots) with presence of scattered Coyote brush individuals. Within each plot, three subplots were sampled. Twelve isolated *Baccharis* individuals (bottom left image) were selected from each subplot based on satellite imagery, four of each size category: large, medium and small. A total of 216 individuals of *Baccharis* (2 sites x 3 plots x 3 subplots x 12 individuals) were selected.

The HHS site (37.40°N, 122.23°W) is a 480-ha research preserve located in the foothills of the Santa Cruz Mountains. The LHS site (37.41°N, 122.18°W) is located east from the HHS site and covers 560 ha (Fig. 1). Both sites have a coastal Mediterranean climate, with warm, dry summers and cool, wet winters. Mean annual precipitation is 605 mm and average daily temperatures range from a minimum of 2 to 4 °C in winter to a maximum of 25 to 27 °C in summer (Zavaleta & Kettley, 2006). Oak-dominated systems (woodlands and savannas) are the most common vegetation types in both sites. Oak systems are dominated by an evergreen oak tree, coast live oak (*Quercus agrifolia* Née), and two deciduous oak species: valley oak (*Q. lobata* Née) in deeper soils, and blue oak (*Q. douglasii* Hook. & Arn.) in shallower, drier soils. Climate, vegetation (oak-dominated systems) and historical land use are similar for both study sites (Palmer, 2003). Livestock (mostly cattle) was removed from HHS site in 1973, and from LHS (study sites) in 1982-1988. Mule deer (*Odocoileus hemionus*) is the main browser and the only ungulate present in both study sites. Western scrub jays (*Aphelocoma californica*) are considered the main avian acorn dispersers in California oak woodlands (Carmen, 2004; Pesendorfer & Koenig, 2016). Tree squirrels (*Sciurus* spp.) are the main terrestrial acorn dispersers in the study area (Perea et al., 2018).

Study species

Coast live oak (*Quercus agrifolia* Née) is an evergreen long-lived tree that grows in lower-elevation oak woodlands of California (Griffin, 1977). Coyote brush (*Baccharis pilularis* DC) is an evergreen, much-branched shrub that grows in shrub communities seral to foothill woodlands of California (Steinberg, 2002). Coyote brush is a colonizer, short-lived and light-demanding shrub species (Hobbs & Mooney, 1986; Zavaleta & Kettley, 2006) that facilitates the recruitment of *Q. agrifolia*, particularly in open woodlands and oak savannas (McBride, 1974; Callaway & Davis, 1998; Zavaleta & Kettley, 2006). Coyote brush is considered a species of very low palatability and nutritious value for grazers and browsers (McBride & Heady, 1968; Smither-Kopperl, 2016), whereas *Q. agrifolia* has been rated fair to poor for mule deer (Sampson & Jespersen, 1963).

Study design

We used a sampling design with Plots and Subplots nested within the fixed factor Site (Fig. 1). For each site (HHS and LHS), we selected three large grassland areas with presence of scattered Coyote brush individuals (plots) and, within each of them, three subplots were sampled (Fig. 1). From satellite imagery, twelve isolated *Baccharis* individuals were selected within each subplot, four of each size category: large (mean shrub diameter>3.5 m), medium (mean diameter 1.5-3.5 m) and small (mean diameter <1.5 m). Therefore, a total of 216 individuals of *Baccharis* (2 sites x 3 plots x 3 subplots x 12 individuals) were selected and their GPS coordinates registered. *Baccharis* were selected so that at least 80% of their surrounding area was covered by grass cover (open microsite) to ensure "edge effects" and statistical independence. Subplot size was approximately 500-900 m^2, with homogeneous ecological conditions (soil type, topography and vegetation).

In the field, the total nurse-plant canopy cover for each individual was calculated based on its perpendicular crown diameters. We also recorded the percentage of the cover that was efficiently protecting the shrub as the shape of the shrub was highly variable. Beneath the canopy of each sampled nurse plant and in a 5 meters concentric area surrounding it, we recorded all young oaks (< 5 cm DBH, diameter at 130 cm height) and measured: 1) height and basal diameter to the nearest millimeter; 2) herbivory damage produced by mule deer distinguishing between 6 different browsing intensities in a 0-5 scale, following Perea et al., (2015): 0=No browsing evidence; 1=Light browsing, with <10% twigs browsed; 2=Low browsing, with 10-30% of twigs browsed; 3=Intense browsing (30-60% of the twigs); 4=Heavy browsing (>60% of the twigs), with clear modification of plant shape; 5=Maximum browsing (>90% of the twigs browsed); 3) microsite location (under the nurse plant vs. open), and 4) distance to the nurse-plant edge in cm. Young oaks were classified in two categories: seedlings (basal diameter <10 mm) and saplings (basal diameter ≥ 10 mm) following previous studies in oak savannas (López-Sánchez et al., 2014; Perea et al., 2016). In addition, groups of deer pellets were also counted in the 5 meters concentric area outside the nurse plant to control for differences in herbivory pressure between plots. Finally, we measured the distance from each nurse plant to the nearest adult *Quercus agrifolia* using a handheld laser distance meter (Leica DISTO^{TM}).

To calculate the density of young oaks under the nurse plant, we divided the number of young oaks by the area efficiently protected by the nurse plant (area of perpendicular crown diameters corrected by the shape of the nurse plant). Density of young oaks in the 5 m concentric area outside the nurse plant was also calculated. To calculate the area outside the target nurse plant, we subtracted any other type of cover (e.g. rock cover, small shrubs) to only account for grasslands. The total area of each nurse plant and its 5 meters surrounding was calculated with GIS software (ArcGis 10.3).

Finally, based on high-resolution historical aerial imagery available in the HHS site, we estimated the minimum age of each *Baccharis* to assess the relationship between nurse-plant size and age. We defined the minimum age of a *Baccharis* as the number of years elapsed from the first time each target shrub was detected in the historical aerial imagery. All nurse shrub individuals were easily detected through aerial imagery in their first years (3-5 years of age; Zavaleta & Kettley, 2006) since all these plants established in open microsites and were, therefore, highly visible. Thus, age was estimated as the first date that an individual appears in an aerial photograph plus 4 years, following the procedures of Zavaleta & Kettley (2006).

Statistical analysis

All statistical analyses were performed using the R statistical software R (Version 3.4.3; R Core Team, 2018). Each *Baccharis* individual (under shrub) and the 5-m surrounding area (open microsite) of each target shrub was the study unit. We first analyzed whether there were differences in overall young oak densities (quantity component) between microsites (open vs. under nurse plant) and sites (HHS vs. LHS). The response variable was oak recruit density calculated as the number of young oaks per hectare, obtaining two values for each target *Baccharis* (density under the nurse plant and density in the open, outside the nurse plant). We used zero-inflated distributions as tree recruitment is often characterized by an excess of zero count (Gómez-Aparicio et al., 2009; López-Sánchez et al., 2016). Therefore, the number of recruits per hectare was assumed to follow a zero-inflated Poisson (ZIP) distribution (Lambert, 1992). Hence, we modelled oak recruitment density as the result of two elements: 1) the probability of recruitment occurrence with the distance to the nearest adult coast live oak tree using a binomial model and 2) the differences in oak recruit density among microsites and herbivore stress (HHS vs. LHS), using a Poisson model. We used the function "zeroinfl" from the R package "pscl". Afterwards, we used the Vuong test (Vuong, 1989) to compare the fit of zero-inflated model with an ordinary Poisson regression.

We analyzed occurrence of nurse-plant facilitation using a Generalized Linear Mixed Model (GLMM), with binomial error structure and logit link using the function glmer of the R package "lme4". We assumed that the nurse plant was facilitating oak regeneration when oak recruit density under the target shrub was higher than in the surrounding 5 m concentric area. The response variable was binary (value of 1 when density of young plants under the nurse plant exceeded the oak density in the surrounding area, and 0 in the opposite situation). Individuals with no recruits at all (under and outside the shrub cover) were discarded from the analysis. Predictors in the model were nurse-plant size (mean crown diameter), herbivore stress (HHS vs. LHS) and their interaction. Subplots nested within plots were introduced as random effect. In addition, to analyze the effect of nurse-plant age on oak facilitation (only in HHS site), we fitted a polynomial term (square) to model the non-linear relationship between nurse-plant size and age. Plot and subplot were also included as random factors.

To examine the effect of nurse-plant size on oak recruit quality, we first calculated the height to diameter ratio (H/D) for each young oak. We used H/D ratio as a proxy of plant growth quality because H/D is considered an important measure of stability and proper plant development in woody plants (Kamimura & Shiraishi, 2007; Schelhaas, 2008; Vospernik et al., 2010). Thus, in herbivore-dominant environments, young plants with lower H/D ratio indicate heavier browsing and inadequate development (e.g., more compact and brush-shaped; Martínez & López-Portillo, 2003) and, therefore, their transition to adult stages is retarded or suppressed (Bartolome et al., 2002; López-Sánchez et al., 2016).

To analyze whether there were differences in oak growth quality among microsites (under nurse plant vs. open) and herbivore stress (HHS vs. LHS), we performed a Linear Mixed Model (LMM) with H/D as the response variable and plot and subplot as random structure. Predictors were microsite, herbivore stress level and their interaction. Then, we calculated the relationship between H/D ratio and browsing damage to assess whether changes in H/D ratio could be attributed to herbivory damage or not. We performed this second model because higher H/D inside the nurse plant might also be attributed to an elongation response of the plant due to reduced insolation. Hence, we only attributed significant differences in plant growth quality to deer herbivory when H/D showed a significant relationship with browsing damage.

In addition, to analyze the effect of nurse-plant size on the recruit quality we performed a LMM with H/D as response variable. Predictors were nurse-plant size, microsite (under nurse plant vs.

open) and herbivore stress (HHS vs. LHS) and their two-way interactions (fixed factors). Subplots nested within plots were introduced as random effects. Similarly, we built another LMM with H/D as response variable and the following predictors: distance to the nurse-plant edge, herbivore stress and microsite and their two-way interactions.

All possible models derived from the maximal models described above were ranked based on the weighting provided by the Akaike information criterion (AIC) using the function “dredge” from the R package “MuMIn”. When there were multiple candidate models with ΔAIC<2, we selected the best-fitting model with the least number of parameters following the principle of parsimony (Burnham & Anderson, 2002). Diagnostic plots were performed to detect heteroscedasticity in the models and qqplots to detect skewness in the model residuals. Finally, predictions were obtained using the “predict” function from the package “stats”.

RESULTS

Deer pellet densities were higher in HHS plots (243, 293 and 341 groups/ha) than in the LHS plots (26, 42, 54 groups/ha). This polarized results justified the use of Site as a proxy for herbivore stress (HHS and LHS).

Overall quantitative component of the facilitative process

The zero-inflated model showed significant differences in young oak density between microsites (open vs. under the nurse plant; Table 1) and herbivore stress (HHS vs. LHS; Table 1), with an overall decrease in the recruit density at increasing distances from the nearest adult tree (Table 1). For both sites (HHS and LHS), young oak density was significantly higher under the nurse plant than in the open microsite. However, the difference in oak density between microsites was more accentuated in the HHS than in the LHS (25 vs. 19 times greater, respectively).

Table 1. Summary of the Zero-inflated Model fitted to analyze the differences in density of young oak seedlings (nº of recruits/ha) between microsites and sites with different herbivore stress (HHS vs. LHS). Firstly, the probability of recruitment occurrence with the distance to the nearest adult tree was modelled using a binomial modeled (below) and secondly the differences in oak recruit density among microsites and herbivore stress (HHS vs. LHS) was modeled using a Poisson model (above).

Count model coefficients (Poisson with log link)				
Predictors	*Coeff.*	*SE*	*z*-value	*P*
Intercept	8.432	0.004	2355.77	**<0.001**
MICROSITE				
Open (against under nurse plant)	-2.930	0.010	-296.29	**<0.001**
HERBIVORE STRESS				
High herbivore stress (HHS) against LHS	-0.106	0.005	-23.17	**<0.001**
MICROSITE × HERBIVORE STRESS				
Open × HHS	-0.302	0.019	-16.10	**<0.001**

Zero inflation model coefficients (binomial family with logit link)				
Predictors	*Coeff.*	*SE*	*z*-value	*P*
Intercept	0.482	0.187	2.581	**0.010**
Distance to adult tree	0.021	0.007	2.918	**0.004**

Overall qualitative component of the facilitative process

We found that seedlings and saplings were browsed by deer differently, being saplings more heavily browsed than seedlings when located in the open microsite (mean browsing damage ± SD: 3.39 ± 0.92 and 0.65 ± 1.09, respectively). Therefore, we decided to analyze seedlings (n=209) and saplings (n=97) separately.

Seedlings at the higher herbivore stress site (HHS) showed no significant differences in height to diameter ratio (H/D) between microsites (t=-1.56, p=0.120; Fig. S1a) whereas at lower herbivore stress (LHS site), seedlings presented significantly higher H/D ratio in the open than under the nurse plant (t=2.04, p=0.0431; Fig. S1a). However, this difference in H/D could not be attributed to herbivory stress because the relationship between browsing damage and H/D in seedlings was not significant in the LHS site (t=-1.09, p=0.278; Fig. S1b).

Conversely, for saplings, at both levels of herbivore stress (HHS and LHS) we found significantly higher H/D ratios under the nurse plant than in the open (Fig. S1c). In addition, differences in H/D between microsites were stronger in the HHS site (t=-6.40, p<0.001; 2.2-fold greater H/D ratio under the nurse plant) than in the LHS site (t=-2.46, p=0.016; 1.36-fold greater H/D ratio under the nurse plant; Fig S1c). Finally, the significant relationship between browsing damage and H/D ratio at both sites (t=-9.92, p<0.001) confirmed that the decrease in H/D ratio for saplings was correlated with an increase of browsing damage (Fig. S1d).

Quantitative differences in facilitation depending on nurse-plant size and distance to nurse-plant edge at contrasting levels of herbivory stress

Occurrence of plant facilitation (i.e., the probability of having higher oak density under the nurse plant than in the open) strongly increased with increasing nurse-plant size (t=3.87; p<0.001; Table 2; Fig. 2).

Table 2. Summary of the selected binomial GLMM to analyze the probability of plant facilitation in relation to nurse-plant size (mean crown diameter) and its variation between sites with different herbivore stress levels (HHS vs. LHS). Response variable was binary (value 1 when density of young plants under the nurse plant exceeded the oak density in the surrounding area, and 0 in the opposite situation).

Explanatory variable	Estimates	Standard error	*t*-value	*P*
Intercept	-3.15	0.80	-3.92	**<0.001**
NURSE-PLANT SIZE	0.66	0.17	3.87	**<0.001**
HERBIVORE STRESS				
High herbivore stress (HHS) against LHS	1.53	0.55	2.81	**0.005**

Bold type indicates a significant effect (P<0.05).

Furthermore, the effect of nurse-plant size on the quantitative component of plant facilitation also varied with herbivore stress (Fig. 2). Thus, the threshold size at which the nurse plant started to be an efficient facilitator (probability of facilitation > 0.5; Fig. 2) was approximately half at high herbivore stress (HHS site) as compared to LHS site (ca. 2.4 vs. 4.7 meter nurse-plant mean diameter; Fig. 2).

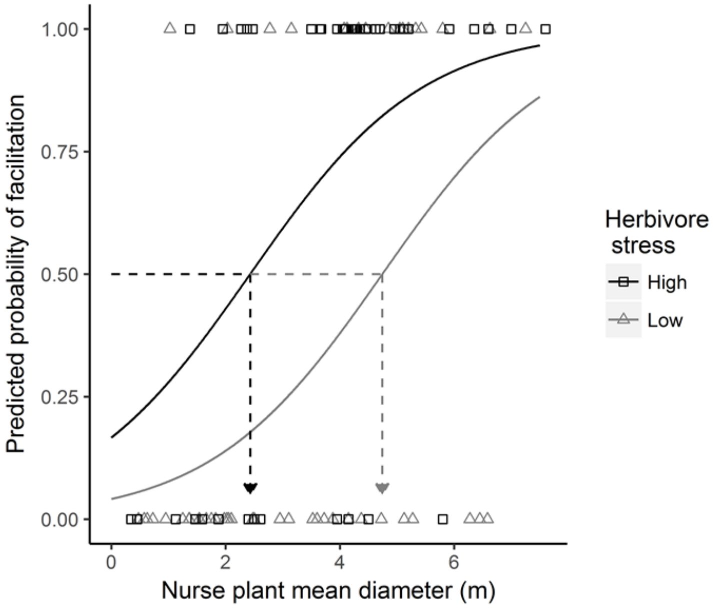

Fig. 2. Predicted probability of plant facilitation as a function of nurse-plant size (mean crown diameter) at high (HHS; black lines) and low (LHS; grey lines) levels of herbivory. Arrows represent the threshold nurse-plant size at which facilitation probability is 50%.

Similarly, distribution of beneficiaries underneath the nurse plant depended on the herbivore stress (Fig. 3). Thus, at low herbivore stress (LHS site), recruits were found significantly closer to the nurse-plant edge as compared to those located at the HHS site (t=-2.19 p=0.030; Fig. 3).

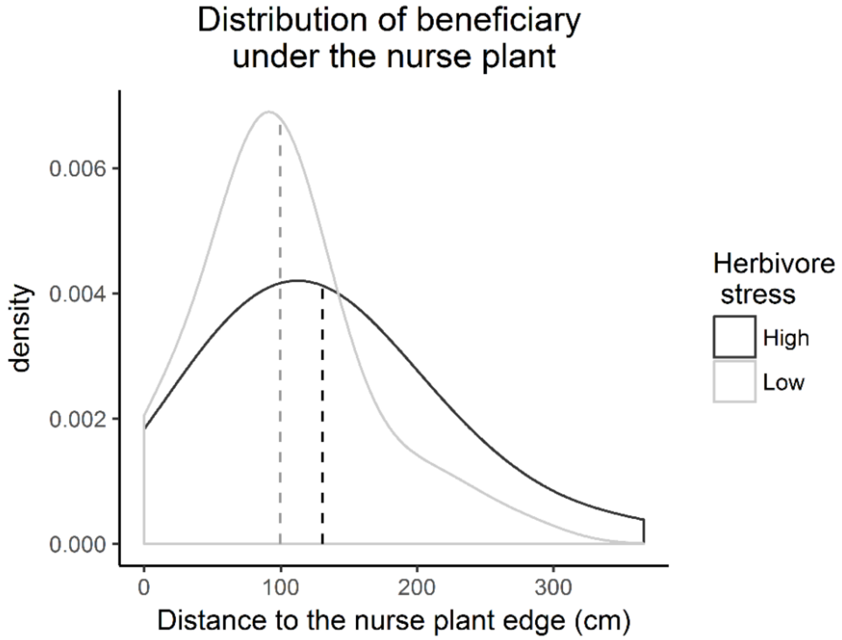

Fig. 3. Kernel distribution of recruits (seedlings and saplings) under the nurse plant for high (HHS) and low (LHS) herbivore stress. Distribution of beneficiaries is shown in relation to distance to the nurse-plant edge. Dashed lines indicate the beneficiary mean distance to the edge for HHS and LHS.

Qualitative differences in facilitation depending on nurse-plant size and distance to nurse plant edge at contrasting levels of herbivory stress

Nurse-plant size was positively associated with plant quality (H/D ratio) of saplings (Table 3; Fig. 4), regardless of the herbivore stress level.

Therefore, under the nurse plant, for each meter increase in nurse-plant diameter, we observed a 6.06 units increase in H/D ratio (t= 4.81; p<0.001; Table 3). In contrast, nurse-plant size had no effect on plant quality in the open microsite (t=0.38, p=0.704).

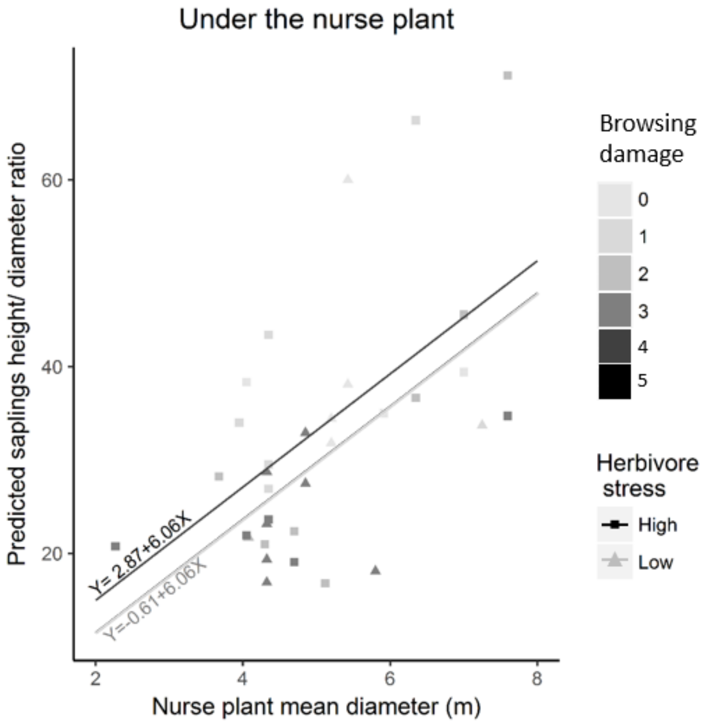

Fig. 4. Predicted H/D ratio for saplings located under the nurse-plant microsite in relation to nurse-plant size at high (HHS; black lines) and low (LHS; grey lines) herbivore stress. Square and triangles represent measured H/D ratio of saplings in HHS and LHS respectively. Color scale represents browsing damage recorded for each individual sapling.

Table 3. Summary of the selected GLMM to analyze sapling growth quality (H/D ratio) as a function of nurse-plant size (mean crown diameter), microsite (open against nurse plant) and sites with different herbivore stress levels (HHS against LHH).

Explanatory variable	Estimates	Standard error	*t*-value	*p*-value
Intercept	-0.61	6.80	-0.09	0.928
NURSE-PLANT SIZE	6.06	1.26	4.81	**<0.001**
MICROSITE				
Open against nurse plant	23.36	7.13	3.28	**0.002**
HERBIVORE STRESS				
High herbivore stress (HHS) against LHH	3.48	3.20	1.09	0.337
NURSE-PLANT SIZE × MICROSITE				
Nurse-plant size × Open	-6.29	1.40	-4.48	**<0.001**
HERBIVORE STRESS × MICROSITE				
HHS × Open	-9.89	3.84	-2.57	**0.012**

Bold type indicates a significant effect (P<0.05).

In addition, H/D ratio of saplings growing underneath the nurse plant was positively correlated with distance to the nurse-plant edge (H/D (under nurse plant) = 0.10 × distance to nurse-plant edge (std. error = ±0.008); t=5.63, p<0.001; Table 4; Fig. 5).

Table 4: Summary of the selected GLMM to analyze differences in H/D ratio of saplings in relation to the distance to the nurse-plant edge, microsite (open vs. nurse plant) and sites with different level of herbivore stress (HHS vs. LHS).

Explanatory variable	Estimates	Standard error	*t*-value	*p*-value
Intercept	47.52	4.06	11.71	<0.001
DIST. TO EDGE	0.10	0.02	5.63	**<0.001**
MICROSITE				
Open against nurse plant	-26.40	4.13	-6.39	**<0.001**
HERBIVORE STRESS				
High herbivore stress (HHS)	-1.79	3.57	-0.50	0.643
DIST. TO EDGE × MICROSITE				
DIST. TO EDGE × Open	-0.09	0.02	-4.35	**<0.001**
SITE × MICROSITE				
Open × HHS	-4.60	3.74	-1.23	0.222

Bold type indicates a significant effect (P<0.05).

Thus, saplings located further inside the nurse plant showed greater H/D ratios. As expected, H/D ratios of saplings located in the open microsite showed no correlation with distance to nurse-plant edge (H/D (open) = 0.016 × dist. nurse-plant edge (std. error = ±0.008); t=1.93, p=0.057; Fig. 5). Additionally, we found significant differences in sapling quality between HHS and LHS in the open microsite, while these differences were rendered under the nurse plant (Table 4; Fig 5).

Fig. 5. Predicted H/D ratio for saplings in relation to the distance to the nurse-plant edge for both microsites (open and under nurse plant) and for high (HHS) and low (LHS) herbivore stress. Square and triangles represent measured H/D ratio of saplings in HHS and LHS, respectively. Color scale represents browsing damage recorded for each individual sapling.

Seedlings performed differently in terms of plant quality as no significant relationship was found between H/D ratio and nurse-plant size or distance to the nurse-plant edge (Fig. S2).

Relationship between size and age of nurse plant

Finally, we found a significant second polynomial relationship between nurse-plant age and size (Predicted nurse-plant size=0.13+0.55*Age-0.017*Age^2; Fig. S3). At approximately 16 years old, nurse-plant size peaked and then started to decrease (Fig. S3).

DISCUSSION

Our results show that both components of plant facilitation (quantity and quality of oak recruits) improved with increasing nurse-plant size. However, contrary to other studies that attributed the increased facilitative effect mostly to the amelioration of abiotic conditions under larger nurse plants (Pugnaire et al., 1996b; Tewksbury & Lloyd, 2001), we pose that, in ungulate-dominated environments, herbivore stress strongly mediates in the observed effect.

For both levels of herbivore stress, we found that, quantitatively, the recruit density increased with nurse-plant size. Only large nurse plants allowed plant facilitation, with greater regeneration densities underneath as compared to microsites located outside the nurse plant. This agrees with previous studies showing that plant facilitation mostly occur under nurse plants of sufficient size (Pugnaire et al., 1996b; Drezner, 2006; Smit et al., 2006; Perea et al., 2016). However, our results highlight that the net effect of nurse-plant size is strongly mediated by the level of the biotic stress. Thus, at high levels of herbivore stress, the probability of facilitation occurrence (i.e., higher recruit density underneath than outside the nurse plant) started in nurse plants of approximately half size (2.4 m crown diameter) than in those located at low levels of stress (starting at 4.7 m crown diameter). These results reveal that, even though nurse-plant size is important in plant facilitation at low and high biotic stress, the magnitude of the effect was strongly mediated by the intensity of herbivory. Therefore, facilitation was more pronounced and required smaller nurse-plant sizes at higher levels of biotic stress. These findings support the predictions of the SGH as the net effect of plant facilitation increased for greater levels of biotic stress but facilitative effects were strongly dependent on nurse-plant traits. This is also consistent with the growing evidence indicating that plant facilitation is strongly dependent on the physical and chemical traits of the nurse plant (Bruno, Stachowicz, & Bertness, 2003; Baraza et al., 2006; Perea & Gil, 2014b). Accordingly, we found a trait-based threshold for nurse plants to provide facilitation but, importantly, that threshold was strongly dependent on the stress level. This trait-based framework may explain why some studies found no facilitation at extreme biotic conditions (Smit et al., 2007; Vandenberghe et al., 2009) where plant traits are disrupted or thresholds are not reached. Our results suggest that facilitation is highly context-dependent with a strong hierarchical effect of plant traits over the biotic stress level. These ideas are indeed consistent with Maestre et al. (2009), who have sought to place the complexity and species-specificity of plant-plant interactions along biotic and abiotic stress gradients.

Similarly, recruit quality improved with increasing nurse-plant size. Thus, larger nurse plants sheltered recruits with proportionally higher H/D ratios. This ratio, a proxy for plant growth quality used in herbivore-dominated environments (Martínez & López-Portillo, 2003), showed a strong correlation with the measured browsing damage index (Perea et al., 2015). Therefore, as hypothesized, larger nurse plants protected recruits better from herbivory (Hay, 1986; Gómez et al., 2001; Perea et al., 2016) and hence allowed beneficiaries to grow well, with balanced H/D ratios.

In addition, this pattern of greater qualitative facilitation under larger nurse plants was confirmed by the strong positive relationship between recruit quality and distance to nurse-plant edge. Furthermore, quantitative results on the distribution of plants under the nurse plants reflected that recruits were distributed differently depending on the herbivore stress. Thus, at higher herbivore stress, recruits were found, on average, at greater distances from the nurse-plant edge. Other studies have shown a similar pattern of recruit clustering around the nurse-plant base (Valiente-Banuet et al., 1991; Drezner, 2006), which has been mostly attributed to the fact that abiotic stress decreases towards the nurse-plant base (Castellanos et al., 1999). In environments with high herbivore stress, this clustered distribution around the plant base could also be attributed to the higher probability of recruits being browsed at shorter distances from the nurse-plant edge. Thus, both the qualitative and the quantitative facilitative effect notably increased with increasing distance to the nurse-plant edge (i.e., with larger nurse plants), which indicates the importance of considering this parameter in the facilitation process in herbivore-dominated environments.

Interestingly, the relative importance of the qualitative component varied with recruit ontogenetic stage. Thus, for saplings, the qualitative component was more pronounced for increasing distances to nurse-plant edge whereas for seedlings the qualitative component was not associated with distance to nurse-plant edge. This is, indeed, consistent with previous studies that detected a lower browsing damage on seedlings compared to saplings in ungulate-dominated environments (Rao et al. 2003; López-Sánchez et al., 2014; Perea et al., 2016). This lack of relationship between seedlings quality and distance to edge is probably related to the difficulty to detect browsing damage on them, as often herbivory results in the elimination of the aerial part of the recruit. Therefore, for seedlings, the biotic stress can be evaluated through the quantitative component while it is difficult to assess the effect on quality (we found no significant relationship between herbivory damage and H/D for this plant category). He and Bertness (2014) have also argued that exceptions to the SGH may occur when the life-history stage of beneficiary species shifts across different stress conditions. For instance, several studies highlighted that qualitative facilitation (e.g. growth) may be most important at intermediate stress levels (Smit et al., 2007; Holmgren & Scheffer, 2010), whereas others show that quantitative facilitation (e.g. density of regeneration) is greater at highest stress levels (Perea et al., 2017). However, here, we showed that the effect of the same stress conditions may be better evaluated by either the qualitative and quantitative components of plant facilitation at different ontogenetic stages. These results reveal the importance of considering both components (quantity and quality) in plant facilitation studies to fully understand how species interactions change at increasing levels of stress.

Size-age relationship in plant facilitation

As expected, plant age and size were positively correlated until plants reached 16 years old when plants begin to decrease in size. This is consistent with observations of Hobbs and Mooney (1986) who described that after maturity is reached, at approximately 9 years old, a decline in biomass occurs until canopy collapses and shrub dies. Zavaleta and Kettley (2006) already pointed out that *Baccharis* are short-living shrubs that contribute to plant succession in oak-dominated systems. Following the age-size relationship described here (Fig. S1), facilitation started to occur at the approximate age of 7 years (equivalent to ~2.5 m of crown diameter at high herbivory level). However, it remains elusive whether plant facilitation is determined by nurse-plant age, size or a combination of both. It seems reasonable that plant size plays a major role for protection against herbivores rather than age whereas, for abiotic stress, amelioration with age may play a more significant role due to an increase of soil nutrient availability for older plants (Pugnaire et al., 1996b). Here, we found a different pattern of beneficiary plant distribution depending on the herbivore stress. For low levels of herbivory, plants were found on average closer to the nurse-plant edge whereas for high levels of herbivory plants were found further inside. This confirms, that plant size rather than age plays a major role in protecting beneficiaries against herbivory and it also contributes to explain why size threshold for plant facilitation varied with increasing biotic stress level. However, further studies should specifically address size and age effect along biotic and abiotic stress gradients by controlling one of the variables and experimentally manipulating the other. Further work to assess the extent to which the complex interplay of relationships uncovered here occurs in other systems of concurrent biotic and abiotic stress is warranted.

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SUPPLEMENTARY MATERIAL

Figure legends

Fig. S1. Histograms show microsite differences in predicted mean H/D ratio for seedlings (a) and saplings (c) at high (HHS) and low (LHS) herbivore stress. Linear regression represent the relationship of H/D ratio with browsing damage for seedlings (b) and saplings (d) at HHS and LHS herbivore stress. The significance is reported at each herbivore stress site (* $p < 0.05$).

Fig. S2. a) Predicted H/D ratio for seedlings located under the nurse plant microsite in relation to nurse-plant size at high (HHS; black lines) and low (LHS; grey lines) herbivore stress. b) Predicted seedling H/D ratio in relation to the distance to the nurse-plant edge for both microsites (open and under nurse plant) and for high (HHS) and low (LHS) herbivore stress. Square and triangles represent seedlings in HHS and LHS, respectively. Color scale represents browsing damage recorded for each individual sapling (ns = not significant).

Fig S3. Predicted relationship between nurse-plant size and its minimum estimated age (black line). Black squares represent each of the 108 nurse plants measured in the high herbivore stress site.

637 **Figure S1**

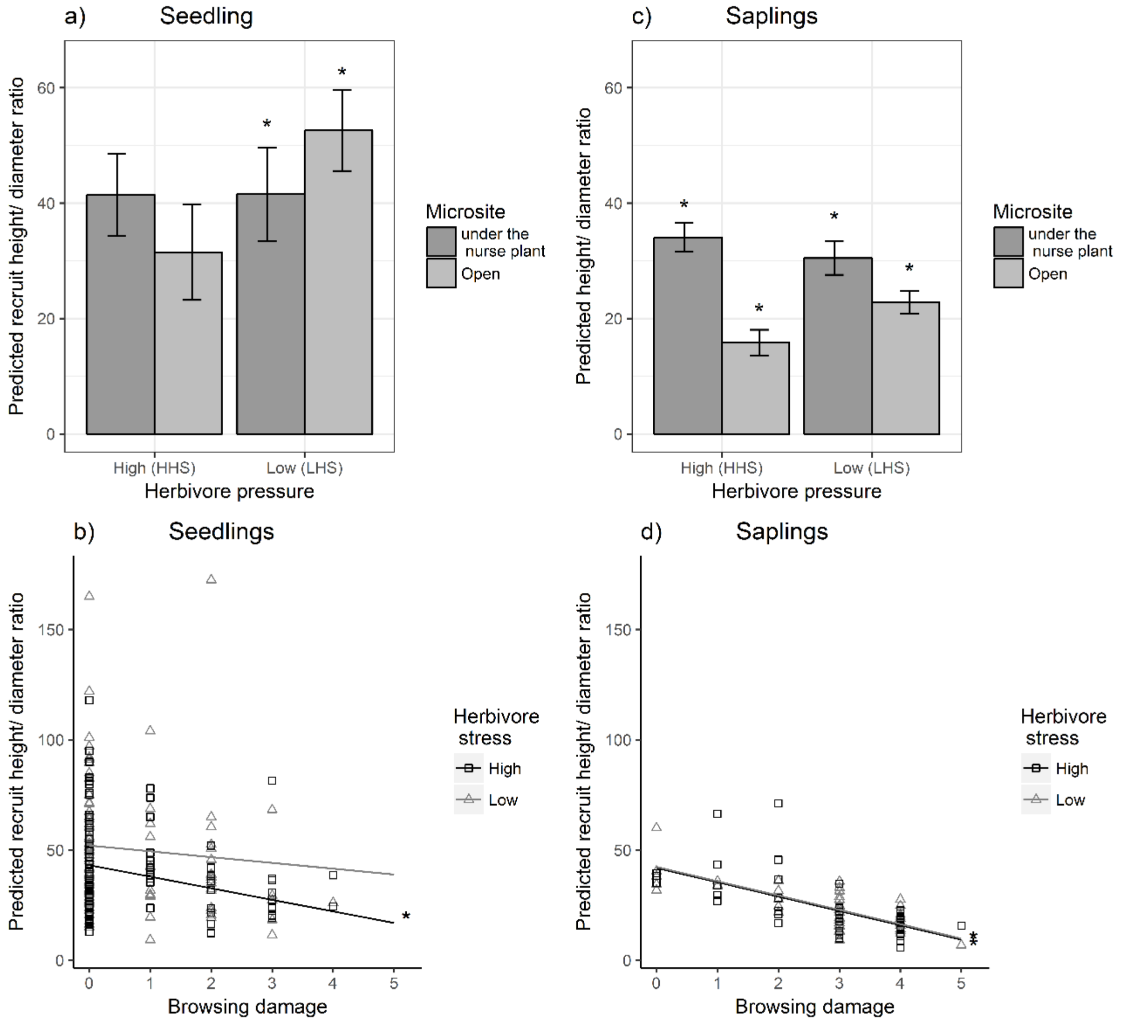

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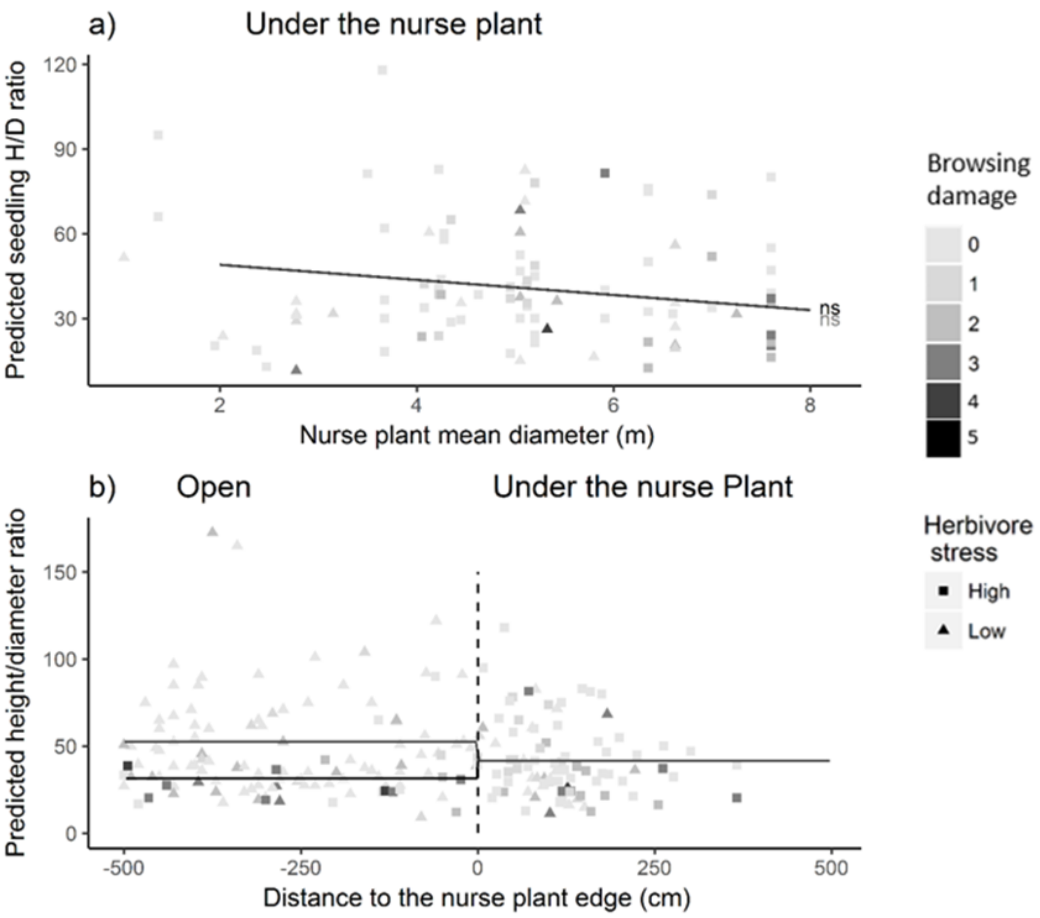
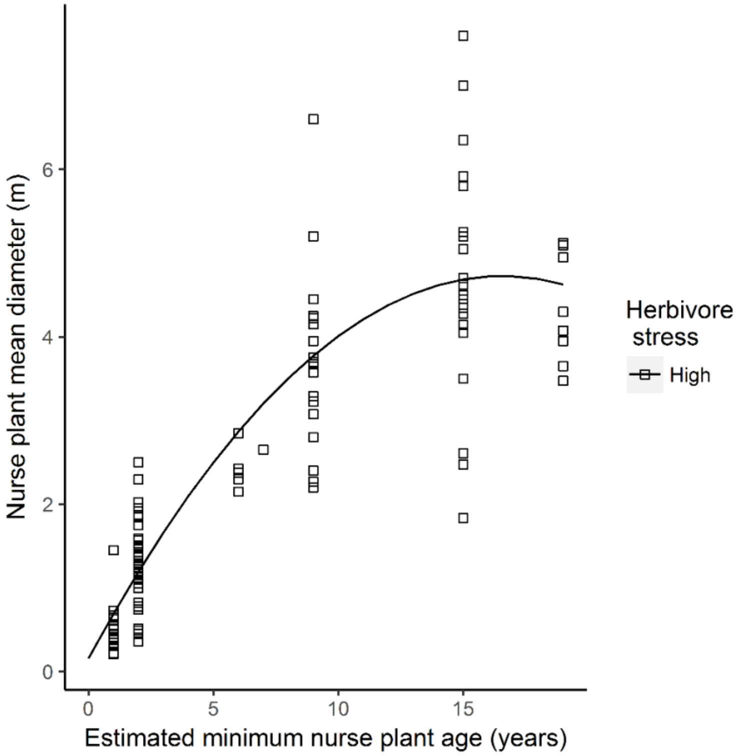
Figure S2


a)
Under the nurse plant
Predicted seedling H/D ratio
120
90
60
30
2
4
6
8
Nurse plant mean diameter (m)
ns
b)
Open
Under the nurse Plant
Predicted height/diameter ratio
150
100
50
0
-500
-250
0
250
500
Distance to the nurse plant edge (cm)
Browsing damage
0
1
2
3
4
5
Herbivore stress
■ High
▲ Low

643 **Figure S3**



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