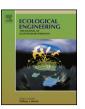
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Research paper

Facilitation among plants: A strategy for the ecological restoration of the high-andean forest (Bogotá, D.C.—Colombia)



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ABSTRACT

Ecosystem invasion by the exotic legume Ulex europaeus (common gorse) impede the establishment of native vegetation by creating a closed canopy and its high resprouting capacity following a disturbance. Over a nine month period, plant-plant interactions between the native legumes, Lupinus bogotensis (shrub) and Vicia benghalensis (herb), and the native tree species Solanum oblongifolium and Viburnum tinoides, were evaluated in a zone close to the Chisacá reservoir in Bogotá, Colombia; that had previously been invaded by *U. europaeus* for at least 60 years. Experimental treatments corresponded to the identity of the native legume species and their sowing densities (high, medium and low), based on distance between individuals: 30, 60 and 90 cm respectively. The native tree species were sown at the same density in all plots (25 individuals, 50 cm between each other). Variables measured in all planted native tree species were: total height, basal diameter and number of leaves or branches. Both native tree species performed best with L. bogotensis at low and medium sowing densities, where the greater establishment of native species indicated a net positive interaction. Growth and survival were higher in all cases when compared with the control plots. There was evidence of facilitation by the native leguminous plants in all the treatments (index of interaction > 0), with the exception of V. benghalensis at high sowing density with S. oblongifolium. We conclude that facilitation between plants can be employed as an effective strategy for the reestablishment of native vegetation and could thereby initiate recuperation of the high-andean forest by reactivating the process of dynamic succession.

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1. Introduction

Plant–plant interaction directly influences ecosystem structure and dynamics, and is responsible for the presence or absence of certain species (Padilla and Pugnaire, 2006). In recent decades, the determinant role of facilitation has been recognized as a positive interaction that directly affects the performance, distribution and metabolism of the species involved (Brooker et al., 2008; Bruno et al., 2003). Negative interactions, in particular competition, have been a central theme in the study of ecology, but it is clear that

organisms can also improve the performance of their neighbors by modifying the environment in a manner that provides benefits for other species (Bertness and Callaway, 1994; Callaway, 2007; Hunter and Aarssen, 1988). For this reason, it is important to expand the study of interaction beyond that of mere competition, and consider also the effects of facilitation for a better understanding of ecosystem and ecological restoration processes.

An example of facilitation between plants is the nurse plant effect, which refers to the positive influence of adult plants on the germination and establishment of seedlings or young individuals under their canopy, effect that occurs because of the amelioration of extreme environmental conditions (Gómez-Aparicio et al., 2004; Holmgren et al., 1997; Padilla and Pugnaire, 2006). The use of certain species as nurse plants with the capacity to modify and improve the environment, within a restoration process in very degraded areas or those of extreme environmental characteristics, increases the probability of achieving rehabilitation and restoration goals (Castro et al., 2002; Padilla and Pugnaire, 2006). For example, this strategy has been used in temperate forests

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(Blanco-García et al., 2011; Dulohery et al., 2000; Yoshihara et al., 2010).

In the study area, the ecosystem of reference is the high-andean forest (located between 2700 and 3300 m asl). This region has had a 150 years old history of intensive use, related mostly with potato cultivation and cattle raising. Also there are forestry plantations of exotic species (*Pinus patula* and *Cupressus lusitanica*) and the presence of the common gorse (*Ulex europaeus*) that was introduced in the 1950s to act as live fencing to protect the area surrounding the reservoir. The gorse is currently one of the main environmental problems in the ecosystem, due to its invasive nature that has lead to the elimination of native plant communities, the local extinction of many species, and the difficulties associated with its control and eradication (León and Vargas-Ríos, 2011). Activities for restoration are therefore urgently required to ameliorate and recover the ecosystems services that native vegetation provides. The study area is part of the rural zone of Bogotá, the capital city of Colombia.

The objective of the present study was to evaluate the effect of two native leguminous species of different habits, a shrub Lupinus bogotensis and the herb Vicia benghalensis, planted at three densities (9, 16 and 81 individuals per plot), on the development of the two native tree species Solanum oblongifolium (Solanaceae) and Viburnum tinoides (Adoxaceae) based on the observed interaction between pairs of species (each legume with each native species). From this, we expected to find evidence of facilitation by the leguminous, mainly by the shrub, at the medium density. In the higher density was more likely to detect competition for the limited space shared by the species, while in the lower density could be no direct or evident effect. In low densities, plants will not fully occupy the growing space available and in high densities may result in intense competition that inhibits the growth and yield of individual plants (Burton et al., 2006; Harper, 1977). A plant with fewer, smaller, or more distant neighbors will have a greater relative growth rate than a similar plant with larger, closer, or more numerous neighbors, and size differences will be enhanced over time (Bonan, 1988). Interaction between the leguminous and native species was evaluated by measuring growth parameters. Based on this approach, the following hypotheses were proposed: (i) L. bogotensis and V. benghalensis will act as nurse plants of the two native species, (ii) young individuals of S. oblongifolium and V. tinoides will present greater growth in plots of medium density of leguminous, and (iii) the different growth patterns of the leguminous will produce a differential effect on the development of *S. oblongifolium* and *V. tinoides*.

2. Materials and methods

2.1. Site and species of study

Experimental plots were established in an area of 1.23 ha in the proximity of the Chisacá reservoir at El Hato, Usme, Bogotá (3120 m asl, 4°23′02.8" N; 74°09′58.7" W) (Fig. 1, also map in Google Earth on KML). The area was cleared entirely from the invasion of *Ulex* with manual and mechanical removal (rake and plowing with tractor) and controlled burns to prevent its rapid recolonization. The zone has a bimodal pattern of precipitation, with the wettest period between April and July and another peak of high precipitation between October and November. Average precipitation was 707.5 mm in 2009 and 1153.7 mm in 2010 (El Hato weather station). The multiannual average temperature is 10.7 °C (La Regadera weather station, between 2002 and 2004), with highest temperatures occurring between October and May and lowest between June and September. As a result of these patterns, the greatest hydrological deficit is seen in the period December to March, when frosts can occur, severely affecting many of the native species of the region as well as crops. The driest months recorded during this study were December 2010 and January–February 2011.

The reference ecosystem is high-andean forest, with an annual average precipitation of between 900 and 1500 mm and an average annual temperature of between 9 and 12 °C. Typical mature vegetation includes species such as Weinmannia tomentosa, Hedyosmum bonplandianum, Myrsine dependens, Oreopanax bogotensis, Tibouchina grossa, Macleania rupestris and Drimys granadensis, among others (Montenegro and Vargas-Ríos, 2008; Mora et al., 2007). Pioneer species that are ideal for initiating the restoration includes Vallea stipularis, Weinmannia microphylla, Verbesina crassiramea, Viburnum triphyllum and those considered in this study, S. oblongifolium and V. tinoides (Mora et al., 2007).

In this study, the facilitator species or nurse plants are: L. bogotensis, a leguminous and rapid-growing shrub species, with a short life cycle and tolerance to nutrient-poor environments: this species is a nitrogen fixer and forms seed banks in the soil (Ávila and Vargas-Ríos, 2009; Díaz-Espinosa and Vargas-Ríos, 2009). And V. benghalensis, an herbaceous species that features creeping growth and a short life cycle; this species is heliophilous and resistant to drought and frost (Díaz-Espinosa and Vargas-Ríos, 2009). The beneficiary species are: S. oblongifolium, a pioneer tree of andean distribution; this species is zoochorous, produces many seeds of high viability and rapid germination and can grow on the edges of roads and exotic plantations (Ávila and Vargas-Ríos, 2009), and V. tinoides, a late pioneer tree of andean distribution; this species can grow up to eight meters in height, is perennial, heliophilous and ornithochorous (Barrera-Cataño et al., 2010). All species were propagated in a nursery using seeds taken from local plants, and later transplanted in the plots. Species and study site in different times of the research are shown in Fig. 2.

2.2. Experimental design and data analysis

Fifty-two $3.5 \,\mathrm{m} \times 3.5 \,\mathrm{m}$ plots were established throughout the zone, providing a total experimental area of 637 m². In each plot a combination of each leguminous species (L. bogotensis-V. benghalensis) with each native species (S. oblongifolium–V. tinoides) was sown, varying the sowing distance (and therefore the planting density) between leguminous individuals. The two native species were sown at the same distance (50 cm) between individuals in all plots, giving a density of 25 individuals in each case, with two control plots per species. The treatments correspond to each leguminous species and its density in relation to the sowing distance between individuals (Table 1), distribution of treatments in plots was aleatory. In control plots only the native species were sown at the density mentioned above. In the whole experiment 650 individuals of each native species were sown, along with 848 individuals of each leguminous species, making a total of 1300 native and 1696 leguminous individuals.

Over a nine month period (October 2010–June 2011), the following variables were recorded from each individual of *S. oblongifolium* and *V. tinoides*: height (cm), measured from the base of the stem to the tip of the longest leaf; diameter (mm), taken at the base using a caliper; and number of leaves in *Solanum* and branches in *Viburnum*. Analysis of the data for each of the variables was performed with time series analysis in a mixed effects model. All analysis was conducted using the statistical package R 2.14 (R Development Core Team, 2011).

The interaction between two plants, either conspecific or not, is typically derived from differences between individuals growing alone vs. growing with other plants (Armas et al., 2004). The magnitude of this interaction can be estimated by the index of magnitude of interaction RII = (Bw – Bo)/(Bw + Bo). It represents the ratio of the

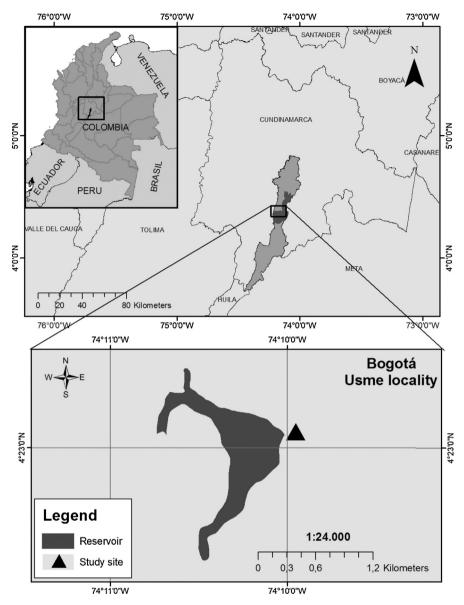


Fig. 1. Map of study site.

Table 1 Experimental treatments: combinations of leguminous and native species.

Treatment	Leguminous	Distance	Density	Native species	No. of plots
1. LupSol 30	L. bogotensis	30 cm	81	S. oblongifolium	4
2. LupSol 60	L. bogotensis	60 cm	16	S. oblongifolium	4
3. LupSol 90	L. bogotensis	90 cm	9	S. oblongifolium	4
4. VicSol 30	L. bogotensis	30 cm	81	V. tinoides	4
5. VicSol 60	L. bogotensis	60 cm	16	V. tinoides	4
6. VicSol 90	L. bogotensis	90 cm	9	V. tinoides	4
7. LupVib 30	V. benghalensis	30 cm	81	S. oblongifolium	4
8. LupVib 60	V. benghalensis	60 cm	16	S. oblongifolium	4
9. LupVib 90	V. benghalensis	90 cm	9	S. oblongifolium	4
10. VicVib 30	V. benghalensis	30 cm	81	V. tinoides	4
11. VicVib 60	V. benghalensis	60 cm	16	V. tinoides	4
12. VicVib 90	V. benghalensis	90 cm	9	V. tinoides	4
Controls	No leguminous present	25 cm.	25	S. oblongifolium–V. tinoides	4 (2 per species)
	TOTAL				52

A. Study Site



B. Research Species



Fig. 2. Study site and research species.

net loss/gain growth due to the interaction (numerator) relative to the growth affected by only facilitative interaction and only competitive interaction (denominator), simultaneously. RII has values ranging from -1 to 1, is symmetrical around zero and is negative for competition and positive for facilitation (Armas et al., 2004). In this case, we used average height of native species individuals in each treatment (Bw) and in the control plots (Bo).

3. Results

S. oblongifolium and V. tinoides had better performance where the leguminous were present (Fig. 3). This trend was more evident

for *S. oblongifolium* growing in the presence of *L. bogotensis*, in plots with medium and low density of the shrub (treatments 2 and 3). Under the microenvironmental conditions created by *Lupinus*, few individuals suffered frost damage; at the end of the cold season only 8% had damage, while in control plots almost all individuals were affected. For *V. tinoides*, *L. bogotensis* was also the best facilitator, but in low density (treatment 6). From the 650 individuals planted of each native tree species, overall survival was 98% for *S. oblongifolium* and 92% for *V. tinoides*. Mortality events occurred during the dry months (December 2010, January and February 2011), that was the period of frost.

The growth of both native species was greater in company of leguminous, mainly with *L. bogotensis*. This shown clearly the

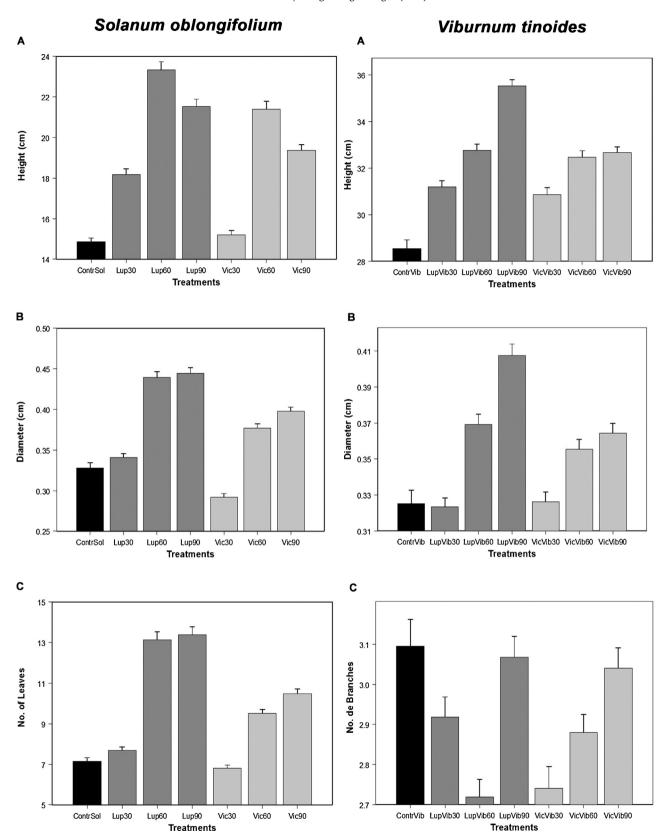


Fig. 3. Average of the growth variables of *S. oblongifolium* and *V. tinoides*: (A) height, (B) diameter and (C) no. of leaves for *Solanum* and no. of branches for *Viburnum*. Bars represent one standard error.

Table 2 Analysis of mixed models for growth variables of *S. oblongifolium*.

Treatments	Variables				
	Height	Diameter	No. of leaves		
1	Non-significant	Non-significant	Non-significant		
2	t = 4.3; $p(192) < 0.001$	t = 5.19; $p(192) < 0.001$	t = 3.93; $p(192) < 0.001$		
3	t = 3.22; $p(192) < 0.001$	t = 3.41; $p(192) < 0.001$	t = 4.13; $p(192) < 0.001$		
7	Non-significant	Non-significant	Non-significant		
8	t = 3.15; $p(192) < 0.001$	t = 2.05; $p(192) < 0.001$	t = 1.30; $p(192) < 0.001$		
9	t = 1.95; $p(192) < 0.001$	t = 3.14; $p(192) < 0.001$	t = 2.02; $p(192) < 0.001$		

Table 3 Analysis of mixed models for growth variables of *V. tinoides*.

Treatments	Variables				
	Height	Diameter	No. of branches		
4	t = 3.64; p(192) < 0.001	Non-significant	Non-significant		
5	t = 5.80; $p(192) < 0.001$	t = 3.67; $p(192) < 0.001$	t = -4.18; $p(192) < 0.001$		
6	t = 9.55; $p(192) < 0.001$	t = 6.85; $p(192) < 0.001$	Non-significant		
10	t = 3.19; $p(192) < 0.001$	Non-significant	t = -3.30; $p(192) < 0.001$		
11	t = 5.38; $p(192) < 0.001$	t = 2.48; $p(192) < 0.05$	t = -2.00; $p(192) < 0.05$		
12	t = 5.64; $p(192) < 0.001$	t = 3.23; $p(192) < 0.001$	Non-significant		

positive effect of the two leguminous that acted as nurse plants, with positive effects on the growth of native species, which exceeds in all cases to that recorded in the control plots (Fig. 3). In the case of *Solanum*, the maximum average height was 23.3 cm, achieved in medium density plots of *Lupinus* (treatment 2), 21.4 cm in medium density plots of *Vicia* (treatment 8), while controls only reached 14.9 cm, taking into account that individuals at moment of be transplanted had an average height of 10 cm. For *Viburnum* maximum average height was 35.5 cm in low density plots of *Lupinus* (treatment 6), 32.7 cm in low density plots of *Vicia* (treatment 12) and 28.5 in control plots, these individuals were transplanted with an average height between 27 and 30 cm. These results also demonstrate that there is a differential effect related with the habit of the facilitators, being more positive the effect of a nurse shrub species.

Results of the mixed model analysis (Tables 2 and 3) for both species and all variables and treatments, bear out the results presented above. For *Solanum*, there was no effect on for any variable in the treatments of high density. While there were significant differences in treatments of medium and low density, that demonstrate an effect in the development related with number and proximity of neighbors. For *Viburnum*, this analysis show more variable results but indicate no effect in high density and positive effect in medium and low density, mainly for height and diameter.

In the case of the index of magnitude of interaction (RII), there is evidence of facilitation in all the treatments (RII > 0), except for *Vicia* at a sowing distance of 30 cm with *Solanum* (treatment 7). The highest RII values coincides to the treatments where the growth variables indicate greater evidence of facilitation; for *S. oblongifolium* with *Lupinus* at 60 cm (treatment 2) and for *V. tinoides* with *Lupinus* at 90 cm (treatment 6). Table 4 shows the index calculated for each treatment.

4. Discussion

Results of this research give evidence that the net effect of the plant–plant interaction between the leguminous species and the two native species was positive, with both leguminous acting as nurse plants, especially in the case of *L. bogotensis*, favoring the development of the native tree species. Contrary to that reported by Ávila and Vargas–Ríos (2009) regarding the negative effect of *L. bogotensis* on the growth of *S. oblongifolium* within clearings in an exotic forestry plantation, this study shows a positive interaction

between these species as observed in the medium and low density plots. The discrepancy between these results could be related to the prevalent light and soil conditions of each study site, as well as the sowing size of individual plants. Conditions in the forest clearings may correspond more closely to those of the high sowing density (30 cm) in this study, where the lowest growth of *Solanum* was recorded (18.2 cm with *Lupinus* and 15.3 cm with *Vicia*, in average), and where the limited entry of light caused by the canopy of the leguminous reduced the availability of this resource to invest in growth.

The growth of *S. oblongifolium* individuals was favored by the modification of the microclimatic conditions within the plots by the leguminous species, such that there was a considerable reduction in the impact of the frosts, to which *S. oblongifolium* has poor tolerance. This mechanism of effecting an improvement to microclimatic conditions is one of the most recognized forms of facilitation (Callaway, 2007; Walker et al., 2007). In ecosystems such as the high-andean forest, it is important to efficiently utilize the resource of light, since the permanently cloudy conditions reduce the effective light available for photosynthesis by these plants. For this reason, shading by a neighboring plant can impede the development of species that are mainly heliophilous, such as *V. tinoides* that demands much more light than the moderately shade-tolerant *S. oblongifolium* (Ávila and Vargas-Ríos, 2009).

Table 4Relative index interaction (RII) values for each combination of leguminous and native species and at each sowing distance.

Treatment	Mean RII	Standard error	
1. LupSol 30	0.068	0.026	
2. LupSol 60	0.181	0.029	
3. LupSol 90	0.153	0.025	
4. VicSol 30	-0.008	0.021	
5. VicSol 60	0.132	0.030	
6. VicSol 90	0.110	0.023	
7. LupVib 30	0.044	0.005	
8. LupVib 60	0.068	0.005	
9. LupVib 90	0.106	0.008	
10. VicVib 30	0.036	0.010	
11. VicVib 60	0.063	0.006	
12. VicVib 90	0.067	0.004	

It is important to note that in this study, *Solanum* is found at the upper limit of its distribution, a situation where facilitation between species is more common (Liancourt et al., 2005). We found meristems of some individuals affected by frosts but when accompanied by nurse-plants they were not completely damaged and, as a result, the majority of those plants that had been considered dead began to resprout once the frosts had passed and many of these grew with greater vigor. This response is very important because resprouting capacity is a mechanism that is fundamental to persistence following a disturbance (Glenn-Lewin and Van der Maarel, 1992) and to enable plants to cope with the frosts in this type of montane ecosystem.

Additional evidence of the positive effects of leguminous species on the native tree species is provided by the fact that the relative interaction index (RII) was greater than zero in the majority of treatments, indicating the existence of facilitation. However, the magnitude of this facilitation varied according to legume type and sowing density. The only case where competition was indicated was the treatment of Vicia at high density with Solanum, which produced a negative RII. This highlight the importance of carefully considering sowing density of nurse plants, since the effects of density experienced by each individual plant depends on the number, size and position of its neighbors (Antonovics and Levin, 1980). The incidence of competition between Vicia and Solanum at high density was expected due to the limited space shared by the two species making access to resources difficult. Because of the climbing behavior of Vicia, in high density plots was very common that individuals of this species were entangled with the leaves and stems of the Solanum and thereby impeding their normal growth.

Although leguminous species used were not adults at the time when the native trees were planted, they can be considered as nurse plants since from the beginning of its development had a positive effect on the growth of Solanum and Vicia. This effect is an example of the positive influence of adult plants on the amelioration of the impact of external environmental factors on seedlings and young individuals (Callaway, 2007; Castro et al., 2002; Gómez-Aparicio et al., 2004: Holmgren et al., 1997: Padilla and Pugnaire. 2006). The balance of the interactions depends not only on the environmental conditions that act upon the species but also on the important influence of their own characteristics, in terms of physiological and ecological optima (Callaway and Walker, 1997; Liancourt et al., 2005), which determine their response to environmental conditions and development within the ecosystem. That is, the vital attributes or life history traits of the interacting species directly influence this balance.

This research shows that the net result of the biological interactions (positive and negative) also depends on the intrinsic characteristics of the species, since S. oblongifolium was observed to behave as a pioneer with rapid growth under favorable conditions enhanced by the presence of the leguminous. On the other hand, V. tinoides is a species of much slower growth that, because it is a late pioneer, requires more stable medium conditions for better development. Consider the responses to abiotic and biotic conditions is necessary because the study of the life history traits associated with tolerance to stress and competitive ability can provide information that enables prediction of the results of facilitation within plant communities (Liancourt et al., 2005). This knowledge can be used to decide how to do combinations of species with different life history traits and growth strategies and therefore can favor successional progress along the desired trajectory.

The advantage of using short life cycle leguminous species as facilitators is that they remain at the ecosystem for a definite period of time, helping the establishment of pioneer species and subsequently providing space for later species. By the time the leguminous disappear, the beneficiary species have already adapted to the medium due to the improved conditions produced by the leguminous and it is thereby possible to naturally reactivate a successional dynamic to which other species of interest can be added, in the form of propagules or individuals. The use of leguminous shrubs in the primary stage of a restoration program, within an herbaceous matrix or on bare soil with the subsequent introduction of trees of interest in a second phase, can be an effective strategy for accelerating the progress of succession (Gómez-Aparicio, 2009). Shrubs as nurse plants are recommended for the restoration of degraded sites where the physical conditions seriously limit the establishment of other species (Padilla and Pugnaire, 2006; Pugnaire et al., 2011).

Although the associations between species evaluated in this study do not occur under natural conditions, they proved to be positive in terms of the establishment of the species of interest and thus demonstrate the plasticity and their ability to adapt themselves to the altered medium conditions. L. bogotensis was the species that performed best in the role of nurse plant or facilitator, as demonstrated by the greater development of both native species when grown alongside. This supports the claim of Gómez-Aparicio (2009), who argues that shrubs are the life form with most potential to act as facilitators in the context of restoration activities because their resource distribution and architecture implies that they do not compete strongly at the soil level. In addition, it is known that certain species of this genus have acted as facilitator species in other ecosystems or under different conditions producing, for example, the positive influence observed on the growth of seedlings of seven high-andean tree species with exclusion of herbivory relative to areas of pasture (Díaz-Espinosa et al., 2007), the facilitator effect of Lupinus elegans on the survival of three native Mexican conifer species (Blanco-García et al., 2011) and the improvement of soil conditions, such as reduction of high surface temperatures and increase of humidity caused by Lupinus lepidus, favoring the two pioneer species Anaphalis margaritacea and Epilobium angustifolium in primary succession (Morris and Wood, 1989).

Regarding V. benghalensis, there have been no previous evaluations of its capacity as a facilitator; however, according to Díaz-Espinosa and Vargas-Ríos (2009), is a species that generates a broad vegetal coverage in very disturbed areas, a feature which can improve certain abiotic factors such as soil organic matter content and contribute to the prevention of erosion of bare soils. Nevertheless, these herbaceous plants could be not a good facilitators since their natural growth is rapid and can limit neighboring species that grow slowly, or are completely heliophilous or are of late succession. Also, not all leguminous shrub species can be considered as facilitators, as shown by this study, *U. europeus* is a leguminous that has an adverse effect on the diversity and function of montane ecosystems in the Andes. It does not have natural consumers and has already altered its population dynamics to adapt to tropical conditions that differ significantly from its natural habitat in Mediterranean ecosystems (León and Vargas-Ríos, 2011).

The results obtained in this study indicate that *S. oblongifolium* was more benefited than *V. tinoides*, supporting the proposal of Liancourt et al. (2005), that species of lower tolerance to abiotic conditions and better ability to respond competitively are those that are facilitated most by their neighbors. Considering that there is currently an urgent need to develop strategies that accelerate the recovery of highly degraded ecosystems (Brooker et al., 2008; Gómez-Aparicio, 2009), the recuperation of native vegetation, even in assisted form, is vital for ecological restoration processes.

In this regard, the study of interactions between species, along with selection of nurse plants, must be considered in planning and execution of conservation and restoration programs, because it constitutes an instrument of great value to achieve reactivation of the successional dynamics and give the desired direction in a disturbed ecosystem.

5. Conclusions

This study gives evidence of facilitation between plants that can be generated within a selected group of species as a restoration strategy. From the first hypothesis: L. bogotensis and V. benghalensis will act as nurse plants of the two native species, results demonstrate that both legumes, mainly L. bogotensis, were nurse plants of the natives, that were beneficiated in their establishment in the study site. Second hypothesis about young individuals of S. oblongifolium and V. tinoides will present greater growth in plots of medium density of leguminous, was confirmed because their growth was higher when they were sown with leguminous species at medium and low densities. At high densities, competition between species was more evident because individuals of native species showed a lower growth. Finally, third hypothesis if the different growth patterns of the leguminous will produce a differential effect on the development of S. oblongifolium and V. tinoides has support. Growth of both native species was greater when sown with L. bogotensis, this shrub has demonstrated a better capacity to ameliorate environmental conditions to favors the natives. Herbs can be more competitive for their fast growing limiting other species.

Positive interactions were confirmed by the estimation of RII that demonstrated dominance of facilitation process in all treatments, except one case (*Vicia* at 30 cm with *Solanum*). Interactions between plants must be estimated and used to plan strategies to restore damaged and altered ecosystems, and facilitation can be used to reestablish some important species that can initiate the succession desired and accelerate the process. Combinations of species of different habits to sown in a disturbed area can avoid competition at initial stages of establishment and the amelioration of microclimatic conditions can favor the development of target species. For the high-andean forest is urgent to develop different restoration strategies to prevent the total extinction of many elements of this ecosystem and loss of its ecological services that are essential for the human communities that depends of these.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2013.04.049. These data include Google maps of the most important areas described in this article.

References

- Antonovics, J., Levin, D., 1980. The ecological and genetic consequences of density-dependent regulation in plants. Ann. Rev. Ecol. Syst. 11, 411–452.
- Armas, C., Ordiales, R., Pugnaire, F., 2004. Measuring plant interactions: a new comparative index. Ecology 85 (10), 2682–2686.
- Ávila, L., Vargas-Ríos, O., 2009. Formación de núcleos de restauración de Lupinus bogotensis dentro de claros en plantaciones de Pinus patula y Cupressus lusitánica. In: Vargas-Ríos, O., León, O., Díaz-Espinosa, A. (Eds.), Restauración ecológica en zonas invadidas por retamo espinoso y plantaciones forestales de especies exóticas. Facultad de Ciencias. Universidad Nacional de Colombia, Bogotá, pp. 234–262.
- Barrera-Cataño, J., Contreras, S., Garzón, N., Moreno, A., Montoya, S., 2010. Manual para la restauración ecológica de los ecosistemas disturbados del distrito capital. Secretaría Distrital de Ambiente and Pontificia Universidad Javeriana, Bogotá, Colombia.
- Bertness, M., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology and Evolution 9, 191–193.
- Blanco-García, A., Sáenz-Romero, C., Martorell, C., Alvarado-Sosa, P., Lindig-Cisneros, R., 2011. Nurse-plant and mulching effects on three conifer species in a Mexican temperate forest. Ecol. Eng. 37 (6), 994–998.
- Bonan, G., 1988. The size structure of theoretical plant populations: spatial patterns and neighborhood effects. Ecology 69 (6), 1721–1730.
- Brooker, R., Maestre, F., Callaway, R., Lortie, C., Cavieres, L., Kunstler, G., Liancourt, P., Tielborger, K., Travis, J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofson, J., Pugnaire, F., Quiroz, C., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present and the future. J. Ecol. 96, 18–34.
- Bruno, J., Stachowicz, J., Bertness, M., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 28 (3), 119–125.
- Burton, C., Burton, P., Hebda, R., Turner, N., 2006. Determining the optimal sowing density for A mixture of native plants used to revegetate degraded ecosystems. Restor. Ecol. 14 (3), 379–390.
- Callaway, R., 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Netherlands.
- Callaway, R., Walker, L., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78 (7), 1958–1965.
- Castro, J., Zamora, R., Hódar, J., Gómez, J., 2002. Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restor. Ecol. 10 (2), 297–305.
- Díaz-Espinosa, A., Vargas-Ríos, O., 2009. Efecto de la siembra de leguminosas herbáceas y arbustivas sobre el control del establecimiento de la especie invasora Ulex europaeus (Fabaceae) en los alrededores del Embalse de Chisacá (Localidad de Usme, Bogotá, D.C.). In: Vargas-Ríos, O., León, O., Díaz-Espinosa, A. (Eds.), Restauración ecológica en zonas invadidas por retamo espinoso y plantaciones forestales de especies exóticas. Facultad de Ciencias. Universidad Nacional de Colombia, Bogotá, pp. 93–130.
- Díaz-Espinosa, A., León, O., Vargas-Ríos, O., 2007. Sobrevivencia y crecimiento de plántulas debajo de Lupinus bogotensis: Implicaciones para la restauración. In: Vargas-Ríos, O., Grupo de Restauración Ecológica (Eds.), Estrategias para la restauración ecológica del bosque altoandino. El caso de la Reserva Forestal Municipal de Cogua, Cundinamarca. Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, pp. 152–172.
- Dulohery, C., Kolka, R., McKevlin, M., 2000. Effects of a willow overstory on planted seedlings in a bottomland restoration. Ecol. Eng. 15 (Supplement), \$57-566
- Glenn-Lewin, D., Van der Maarel, E., 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D., Peet, R., Veblen, T. (Eds.), Plant Succession: Theory and Prediction. Chapman and Hall, London, pp. 12–59.
- Gómez-Aparicio, L., 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. J. Ecol. 97, 1202–1214.
- Gómez-Aparicio, L., Zamora, R., Gómez, J., Hódar, J., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14 (4), 1128–1138.
- Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York.
- Holmgren, M., Scheffer, M., Huston, M., 1997. The interplay of facilitation and competition in plant communities. Ecology 78 (7), 1966–1975.
- Hunter, A., Aarssen, L., 1988. Plant helping plants: new evidence indicates that beneficence is important in vegetation. Bioscience 38 (1), 34–40.
- León, O., Vargas-Ríos, O., 2011. Estrategias para el control, manejo y restauración de áreas invadidas por retamo espinoso (*Ulex europaeus*) en la vereda el Hato, localidad de Usme, Bogotá, D.C. In: Vargas-Ríos, O., Reyes, S. (Eds.), La Restauración Ecológica en la Práctica: Memorias I Congreso Colombiano de restauración Ecológica y II Simposio Nacional de Experiencias en Restauración Ecológica. Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, pp. 474–490.
- Liancourt, P., Callaway, R., Michalet, R., 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology 86 (6), 1611–1618.
- Montenegro, A., Vargas-Ríos, O., 2008. Caracterización de bordes de bosque altoandino e implicaciones para la restauración ecológica en la Reserva Forestal de Cogua (Colombia). Revista de Biología Tropical 56 (3), 1543–1556.

- Mora, J., Figueroa, Y., Vivas, T., 2007. Análisis multiescala de la vegetación de los alrededores del embalse de Chisacá (Cundinamarca, Colombia). In: Vargas-Ríos, O., Grupo de Restauración Ecológica (Eds.), Restauración ecológica del bosque altoandino. Estudios diagnósticos y experimentales en los alrededores del embalse de Chisacá (Localidad de Usme, Bogotá). Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, pp. 16– 103.
- Morris, W., Wood, D., 1989. The role of Lupine in succession on mount St. Helens: facilitation or inhibition? Ecology 70 (3), 697–703.
- Padilla, F., Pugnaire, F., 2006. The role of nurse plants in the restoration of degraded environments. Front. Ecol. Environ. 4 (4), 196–202.
- Pugnaire, F., Armas, C., Maestre, F., 2011. Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradients, and ecosystem function. J. Arid Environ. 75 (12), 1310–1320.
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing, Viena, Austria. http://www.R-project.com
- Walker, L., Walker, J., Del Moral, R., 2007. Forging a new alliance between succession and restoration. In: Walker, L., Walker, J., Hobbs, R. (Eds.), Linking Restoration and Ecological Succession. Springer, New York, pp. 1–18.
- Yoshihara, Y., Sasaki, T., Okuro, T., Undarmaa, J., Takeuchi, K., 2010. Cross-spatialscale patterns in the facilitative effect of shrubs and potential for restoration of desert steppe. Ecol. Eng. 36, 1719–1724.