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Effect of irrigation and pruning on the fog capture ability of Chilean xerophytic formations

Efecto del riego y la poda en la habilidad de captura de niebla de formaciones xerofíticas chilenas

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ABSTRACT

Water availability and herbivory are critical factors limiting plant growth in semi-arid regions. Xerophytes in fog ecosystems, while capable of capturing fog water, are likely constrained by these factors. Given that fog capture is closely tied to vegetation structure in terms of canopy volume, cross-section, and leaf traits, we hypothesized that irrigation and pruning (as a form of controlled herbivory) could enhance fog harvest by stimulating canopy growth. To test this, we evaluated the impact of these management practices on ten xerophytic species across two communities in north-central Chile. We assessed plant responses through cross-sectional growth, branch elongation, and fog drip beneath the canopy. Irrigation promoted cross-sectional growth in two species, while pruning negatively impacted three species. In terms of branch growth, two species responded positively to irrigation, while one was negatively affected by pruning. Fog drip analysis revealed significant treatment effects in less than 11% of species × site × treatment × time combinations, with negative effects prevailing. Interactions between treatments sometimes nullified or altered their effects, indicating that irrigation is necessary for pruning impacts to manifest. As pruning consistently led to negative outcomes, we suggest that intense herbivory may similarly impair shoot growth and fog collection. Overall, our findings indicated that xerophytes do not require irrigation or pruning to sustain their fog capture potential. However, irrigation enhanced growth and vigor in several species, suggesting its potential utility in productive or restoration contexts, particularly when management practices are tailored to species-specific responses.

Keywords: clouds, watering, silvicultural managements, herbivory.

RESUMEN

La disponibilidad de agua y la herbivoría son factores críticos que limitan el crecimiento de las plantas en las regiones semiáridas. Las xerófitas en ecosistemas de niebla, si bien son capaces de capturar esta agua, probablemente estén limitadas por estos factores. Dado que la captura de niebla está estrechamente relacionada con la estructura de la vegetación en términos de volumen del dosel, sección transversal y características de las hojas, planteamos la hipótesis de que el riego y la poda (como una forma de herbivoría controlada) podrían mejorar la recolección de niebla al estimular el crecimiento del dosel. Para probar esto, evaluamos los efectos de estos manejos en diez especies xerófitas en dos comunidades en el centro-norte de Chile. Evaluamos las respuestas de las plantas a través del crecimiento transversal, la elongación de las ramas y el goteo de niebla debajo del dosel. El riego promovió el crecimiento transversal en dos especies, mientras que la poda afectó negativamente a tres especies. En cuanto al crecimiento de ramas, dos especies respondieron positivamente al riego, mientras que la poda afectó negativamente a una. El análisis del goteo de niebla reveló efectos significativos de los tratamientos en menos del 11% de las combinaciones de especie × sitio × tratamiento × tiempo, prevaleciendo los efectos negativos. Las interacciones entre tratamientos a veces anularon o alteraron sus efectos, lo que indica que el riego es necesario para que se manifiesten los impactos de la poda. Como la poda condujo consistentemente a resultados negativos, sugerimos que la herbivoría intensa puede similarmente afectar el crecimiento del vástago y la recolección de niebla. En general, nuestros hallazgos indicaron que las xerófitas no requieren riego ni poda para mantener su potencial de captura de niebla. Sin embargo, el riego mejoró el crecimiento y el vigor de varias especies, lo que sugiere su utilidad potencial en contextos productivos o de restauración, particularmente cuando las prácticas de manejo se adaptan a respuestas específicas de cada especie.

Palabras clave: nubes, riego, manejos silvícolas, herbivoría.

INTRODUCTION

Xerophytic formations are plants that occur in arid and semi-arid zones of the world (Cuevas et al., 2023a). In particular, those inhabiting fog ecosystems may act as natural fog catchers (Stanton et al., 2014; Chung et al., 2017; Cuevas et al., 2023a): they can harvest water from environmental humidity passively, such as fog or dew during cold days or nights (Von Hase et al., 2006). Accordingly, they may take advantage of the harvested water by directing it to the roots or absorbing it directly through the leaves (Boanares et al., 2019) before it evaporates during the day. Because fog capture requires interaction with physical structures (Stanton et al., 2014), there is a widespread notion of the positive influence of vegetation architecture and aboveground biomass on fog interception (Chung et al., 2017; Cuevas et al., 2023a). This interaction is expressed through variables such as leaf area, branch stratification, and canopy biomass, which influence the rate of fog and rain capture and transfer to the soil (Barbosa et al., 2010). Canopy roughness (Chung et al., 2017), cross-section (Ingraham & Matthews, 1988), leaf angle over branches (Squeo et al., 2004), and even leaf surface traits (Cuevas et al., 2023b) are also determinants of fog harvest rates. However, at present, the potential of plants from semi-arid zones for fog harvest seems to be impaired due to anthropogenic deforestation (da Silva et al., 2022). In addition, the introduction of exotic herbivores (rabbits, hares, goats, cattle, horses) and the land use change also produces a major deterioration of the vegetation (Moreira et al., 2021). Grazing is a factor that severely limits plant growth, especially when herbivores overpopulate new areas of colonization (Lightfoot, 2018; Moreira et al., 2021). Also, herbivory interacts with drought, which is another factor limiting plant growth in arid and semi-arid zones (Adejuwon & Dada, 2021; Wu et al., 2024). Although xerophytes from fog ecosystems can be capable of capturing fog water, it is not clear how grazing and drought would affect this capability.

Given the above factors that potentially limit plant growth, we might expect that any management alleviating these limitations could enhance the sustainability of xerophyte aboveground biomass for securing fog capture. Artificial irrigation and pruning are common silvicultural and silvopastoral management practices (Klingeman et al., 2008; Çalişkan & Boydak, 2017).

Water is one of the environmental factors essential for plant productivity, especially in crops. Its relevance in physiological processes determines that plants must replace the lost water, either by rain or irrigation. Irrigation, the artificial application of water to plants through basic or sophisticated systems to meet their needs, aims to increase plant productivity and, in some cases, to ensure the survival of plants that could not thrive if they were not native to the climate and soil of the plantation area. Although agronomic practice especially employs irrigation (Ibrahim et al., 2021), it is also used for wild species plantations (Bown et al., 2018; Oros, 2022). Indeed, irrigation is a necessary step in reforestation of open areas of arid and semi-arid ecosystems (Çalişkan & Boydak, 2017).

On the other hand, pruning is a management practice to remove branches to balance the tree's vegetative and reproductive development and to promote fruit production and quality (Nasrabadi et al., 2022). This practice promotes tissue regeneration and secondary growth (Pallardi, 2008; Riedemann et al., 2016). By eliminating apical dominance, proper shoot management allows shaping the plant architecture, promotes the growth of lateral buds, and ultimately enhances the development of aboveground biomass (Klingeman et al., 2008; Ryder & Moore, 2013). Plant's response to pruning depends on water and nutrient availability, and growth season conditions (Azócar et al., 2001; Ellena, 2012). Therefore, because environmental factors do not act in isolation, studying their interactions with management factors is imperative.

The link between pruning and browsing or grazing in natural environments stems from the fact that we can consider pruning as simulated and controlled herbivory (*sensu* Waterman et al., 2019). Compared with natural herbivory, pruning represents a benefit for both the manager and the plant itself, while animals seek to profit from plant resources, considering their own feeding preferences (Waterman et al., 2019). However, the evidence shows growth compensation or overcompensation after herbivory (Schulte, 2014; Zhu et al., 2019), revealing that plants also benefit from this interaction. Nevertheless, overbrowsing or overgrazing imbalances plant-herbivore interaction, thus, one could expect that controlled pruning should produce better results than uncontrolled herbivory.

Accordingly, we hypothesize that irrigation and pruning can enhance fog capture by xerophytes and promote greater development of aboveground biomass. This is a putative chain of events in which water availability and pruning affect plant structure and, ultimately, fog harvesting, all of which are important links in this chain. Consequently, our objective is to evaluate if experimental pruning and irrigation enhance fog capture of xerophytic shrubs in the coastal zone of the Coquimbo Region, Chile. This topic is valuable to study because xerophytic shrubs contribute to ecosystem services, being key to avoiding soil erosion in semi-arid regions, supporting animal feed and shelter, which makes this vegetation type an object for conservation and regeneration. In addition, improving soil water content could benefit other plant-dependent organisms; xerophytes could also potentially become natural fog catchers, and people should use their harvest for low water demand purposes such as human and animal consumption, agriculture, and forestry at the household level.

METHODS

Study site. We conducted the research at two sites in the Coquimbo Region of north-central Chile. The northernmost site is a coastal steppe shrubland community (Majada Blanca, 30° 03’ 52” S, 71° 19’ 24” W, 670 m a.s.l.), while Los Tomes site is a forest steppe shrubland vegetation (31° 29’ 23” S, 71° 31’ 50” W, 830 m a.s.l.), as representative of the xerophytic formations that populate north-central Chile. The stands are located at the mountaintops that receive fog influence from the nearby Pacific Ocean within arid and semi-arid climates (Montecinos et al., 2016).

Rainfall measured at El Panul weather station (122 m a.s.l.), close to Majada Blanca, averaged 71.3 mm (period 2004–2023). For the Los Tomes site, the nearest weather station was Huentelauquén (22 m a.s.l.), with mean precipitation of 76.1 mm (2018–2023). Specifically, it rained 25.6-105.5 mm (El Panul), and 29.2-100.3 mm (Huentelauquén) for the years when this research was carried out (2021 and 2022, respectively). However, most of the 2022 rainfall occurred as the study was ending; therefore, our results were representative of a dry year.

There were no *in situ* data on soil properties, therefore we obtained the information from nearby sites (Table 1). In Majada Blanca, pH was neutral, the soil was not considered saline, organic matter and nitrogen content were poor compared to more productive soils, but phosphorus and potassium were in good or high levels. No records were available for Los Tomes.

Irrigation and pruning design. Based on their abundance, we selected five woody species for each site. They were part of different families, growth habits, and root architectures. The populations of interest were *ca.* 0.5 ha plots enclosed by a 1.7 m height fence to prevent herbivory by large animals, a major disturbance in the Coquimbo Region (Schulte, 2014). We randomly selected twelve individuals and assigned three plants (true replicates) to each of the following factorial treatments: i) no irrigation, no pruning (−I−P, control); ii) irrigation and pruning applied (+I+P); iii) no irrigation, pruning applied (−I+P); and iv) irrigation applied, no pruning (+I−P). Treatments and replicates were spatially randomized.

We supplied irrigation using water collected from large fog catchers (two units of 150 m^2 in Majada Blanca, and two of 60 m^2 in Los Tomes). We stored water in PVC tanks of 2,350-5,000 L in the northernmost and southernmost sites, respectively. Water was distributed to the experimental sites via 2 cm internal diameter irrigation pipes. Within the plots, the conduction was carried out with 1 cm internal diameter pipes equipped with self-compensating drippers, two units per plant, which delivered 2 L h^{-1} each. We adjusted irrigation time with a battery-powered time programmer. The exact amount of water passing through the system was measured with a volume counter.

Little information was available about the actual water needs of plants (Bown et al., 2018; Oros, 2022). Thus, we could not carry out a species-specific irrigation under precise agronomic criteria (e.g., crop coefficient, evapotranspiration, etc.), and the development of optimal irrigation curves and schedules was beyond the scope of this study. Therefore, we relied on the published literature and adjusted the irrigation system based on an ecological criterion, considering watering with an extra of at least 100% more than its annual natural supply as fog and rain (Table 2 and 3, see Results. *Irrigation treatment*).

Pruning was conducted according to Ellena (2012). Briefly, we carried out pruning with garden scissors on two occasions per site (June 17-18 2021, and March 10-17 2022), ensuring it was uniform within the same species, but varying among species. The pruning dates were close to those Bhatla (2023) pointed out.

Plant growth. We estimated an integrated measure of plant development (i.e., the whole plant), and a branch-level response. The first one considered height, and cross-section, which the literature identifies as being of primary importance for fog interception. The branch study provided a more detailed evaluation of branches covered by leaves, flowers, and fruits, among other vegetative material, which served as sensitive indicators of stress and management.

Every 1.5 months we measured the plant height, and the horizontal major and minor axes of plants (three replicates per treatment) with a metric tape (1 cm resolution)

Table 1. Soil properties (10-30 cm depth) for a site near Majada Blanca, 200 m a.s.l., and 2 km from the main study site. Available element content is reported.

Propiedades del suelo (profundidad 10-30 cm) para un sitio cercano a Majada Blanca, a 200 m s.n.m., y 2 km del sitio de estudio principal. Se reporta el contenido disponible de elementos.

Property	pH	Electrical conductivity	Organic matter	N	P	K	Fe	Zn	Mn	Cu
Unit		dS m^{-1}	%				mg kg^{-1}			
Value	6.9	0.5	1.3	5	16	281	17.0	0.7	9.9	5.5

Source: Collaboration from another project of our team.
Colaboración de otro proyecto de nuestro equipo.

Table 2. Irrigation program for the two experimental sites (Majada Blanca and Los Tomes). Plants were watered with fog via two drippers, each one with a discharge of 2 L h^{-1}.

Programa de irrigación para los dos sitios experimentales (Majada Blanca y Los Tomes). Las plantas fueron regadas con niebla por medio de dos goteros, cada uno con una descarga de 2 L h^{-1}.

Site	Majada Blanca		Los Tomes	
Period	March 2, 2021/ January 8, 2022	January 8, 2022/ July 12, 2022	February 12, 2021/ January 8, 2022	January 8, 2022/ August 22, 2022
Irrigation time per event (min)	45	50	45	45
Irrigation days per week	2	3	2	5
Volume per event (L)	3	3.3	3	3
Volume per week (L)	6	10	6	15
Volume per month (L)	24	40	24	60

Figure 1. Plant specimens subjected to irrigation (A, C) or non-irrigation (B, D); A) and B) correspond to *Oxalis gigantea* (Oxalidaceae) in Majada Blanca, and C) and D) are *Bahia ambrosioides* (Asteraceae) in Los Tomes. Pictures of May 2021.

Especímenes de plantas sujetos a riego (A, C) o no riego (B, D); A) y B) corresponden a *Oxalis gigantea* (Oxalidaceae) en Majada Blanca, y C) y D) son *Bahia ambrosioides* (Asteraceae) en Los Tomes. Fotografías de mayo 2021.

Table 3. Comparison of irrigation with respect to natural water supply from rain and fog.

Comparación del riego con respecto a la provisión natural de agua de la lluvia y la niebla.

Year				2021	2021	2021	2022	2021	2022
Site/Species (family)	Habit[€]	Root architecture[£]	Mean cross-section (m^2) (A)	Mean fog and rain drip (mm year^{-1}) (B)	Mean fog and rain drip (L year^{-1}) (C= A*B)	Annual irrigation (L) (D)	Annual irrigation (L) (E)	Extra supply (%) =100*D/C	Extra water supply (%) =100*E/C
Majada Blanca									
Adesmia microphylla (Fabaceae)	EG	t	2.81	95.1	267.2	288	480	107.8	179.6
Bridgesia incisifolia (Sapindaceae)	D	s	5.02	39.8	199.8	288	480	144.1	240.2
Heliotropium stenophyllum (Heliotropiaceae)	EG	s	6.27	50.8	318.5	288	480	90.4	150.7
Oxalis gigantea (Oxalidaceae)	D	ss	3.15	67.1	211.4	288	480	136.2	227.1
Senna cumingii (Fabaceae)	EG/D	d	0.61	62.0	37.8	288	480	761.9	1,269.8
Los Tomes									
Baccharis vernalis (Asteraceae)	EG	?	2.10	71.9	151.0	288	720	190.7	476.8
Bahia ambrosioides (Asteraceae)	D	s	0.98	70.9	69.5	288	720	414.4	1,036.0
Escallonia pulverulenta (Escalloniaceae)	EG	?	3.74	145.4	543.8	288	720	53.0	132.4
Gochnatia foliolosa (Asteraceae)	EG	?	3.01	109.2	328.7	288	720	87.6	219.0
Puya chilensis (Bromeliaceae)	EG	s	3.12	70.1	218.7	288	720	131.7	329.2

[€] Habit : EG = evergreen, D = summer deciduous (after Squeo et al., 1999; Olivares & Squeo, 1999, and personal observations).

[£] Root architecture: t = taproot, s = shallow, ss = shallow succulent, d = dimorphic (after Squeo et al., 1999; Menceyra et al., 2021).

[€] Hábito: EG = perenne, D = caducifolio de verano (según Squeo et al., 1999; Olivares & Squeo, 1999 y observaciones personales).

[£] Arquitectura radicular: t = raíz pivotante, s = superficial, ss = suculenta superficial, d = dimórfica (según Squeo et al., 1999; Menceyra et al., 2021).

to calculate their cross-section. We applied measurements to common geometric shapes (ellipses and rectangles) using standard formulas.

In addition, we marked three branches on each experimental plant (leaves in the case of the bromeliad *Puya chilensis* Molina), representing subsamples. They were measured every 2.5 months, from the mark position (a colored tag) up to the branch tip, using a small metric tape (1 mm resolution). None of these branches were cut. For the pruned specimens, we placed three additional marks on cut branches if the intervened ones responded to pruning, rather than those we have previously marked.

Fog collection. To determine fog drip beneath each experimental plant, we connected three 14-cm diameter funnels to 1-L bottles and randomly positioned them below the canopy of each plant. We chose this number of funnel-bottle system to ensure a better representativeness of fog throughfall, which was expected to be variable under the canopy, especially for those large sized individuals. The number of funnels was adequate for the cross-section area of shrubs that reached up to 6 m^2 (Table 3), and enabled the calculation of a mean and standard error of the fog harvest, values that served as sample estimations of its parametric population mean. We filled bottles with 0.5 cm of vaseline to avoid water evaporation, and they were collected every month and replaced by other new ones. In the laboratory, we assessed the collected volumes with graduated cylinders. We considered the collected devices as subsamples of the three replicates made up of the shrubs.

Data analysis. Prior to statistical tests, we averaged the subsamples (bottle volumes and branch lengths corresponding to each individual) in order to have a single value for each one of the three individuals analyzed per treatment. We performed analyses for net growth between the beginning and end of the tests (m^2 or cm). After checking the assumptions of normality and homoscedasticity, we applied a two-way Analysis of Variance (ANOVA) to make comparisons among treatments (irrigation and pruning). If the assumptions of normality and homoscedasticity were not met, we transformed the data with the logarithmic function. In a few cases, this issue was not resolved, and then we applied a non-parametric Scheirer-Ray-Hare extension of the Kruskal-Wallis test.

We constructed a time series of fog harvest (millimeters, mm) for every species monthly, representing the treatments as a percentage with respect to the control (−I−P). The latter was always considered as 100%. Notwithstanding, we used the original data when making the two-way ANOVAs. For all analysis, irrigation and pruning effects, as well as their interactions, were evaluated on each date by means of the Statistica 7.0 software (StatSoft, Inc., Tulsa, OK, USA).

RESULTS

Irrigation treatment. To know how much water should be applied to plants, we examined the water drip (fog and rain) under control plants (−I−P) during 12 consecutive months during the year 2021 (Table 3, column B). This drip fluctuated from 40 to 95 mm in Majada Blanca, and from 70 to 145 mm in Los Tomes. Multiplying this water layer by the mean cross-section of 12-15 individuals at the beginning of the study (column A), we obtained the total amount of water deposited under each plant: 38-318 L $year^{-1}$ in Majada Blanca, and 70-544 L $year^{-1}$ in Los Tomes (column C). These volumes were compared with the irrigation applied in the year 2021 (288 L $year^{-1}$). Accordingly, the extra amount of water applied as irrigation was 53% (*Escallonia pulverulenta* (Ruiz & Pav.) Pers. var. *pulverulenta*) to 762% in *Senna cumingii* (Hook. & Arn.) H.S. Irwin & Barneby. This large difference was due to the lowest cross-section of the latter species that determined a small natural water harvest compared to the irrigation. Irrigation increased during 2022, reaching 150-1,270% (Majada Blanca) and 132-1,036% (Los Tomes) more water than the natural capture.

Qualitatively, there were species that showed evident response to irrigation (Figure 1). *Oxalis gigantea* Barnéoud (Figure 1A, watered) exhibited a greater density of leaves and a much lesser lichen coverage versus a non-watered *O. gigantea* (Figure 1B). We observed similar trends in Los Tomes (i.e., *Bahia ambrosioides* Lag., Figures 1 C, D). Strikingly, some species showed an aspect resembling dead individuals, without leaves, but they re-sprouted after irrigation (i.e., *Bridgesia incisifolia* Bertero ex Cambess.).

Response of cross-section to irrigation and pruning. In Majada Blanca, there were no significant effects for *Adesmia microphylla* Hook. & Arn. despite control plants having the largest size variation between the beginning and the end of the experiment (Figure 2A). Neither effect for *Bridgesia incisifolia* was detected (Figure 2B).

Heliotropium stenophyllum Hook. & Arn. showed narrow size variation that could not be discriminated against by the experimental treatments (Figure 2C). Conversely, *O. gigantea* did show irrigation and pruning effects, where watering favored growth, and pruning negatively impaired it (Figure 2D). +I−P was the best treatment for *O. gigantea*. We found a similar pattern in *Senna cumingii*, but with no statistical significance (Figure 2E). In *O. gigantea*, the interaction between the two variables meant that the effect of pruning could only be observed in irrigated plants (Figure 3A).

Los Tomes showed species with significant patterns, except for *Baccharis vernalis* F.H. Hellwig and *Puya chilensis* (Figures 2F, J). *Bahia ambrosioides* had a significant interaction that canceled the main effects (Figures 2G, 3B). *Escallonia pulverulenta* cross-section growth was favored by irrigation, while pruning was detrimental (Fi-

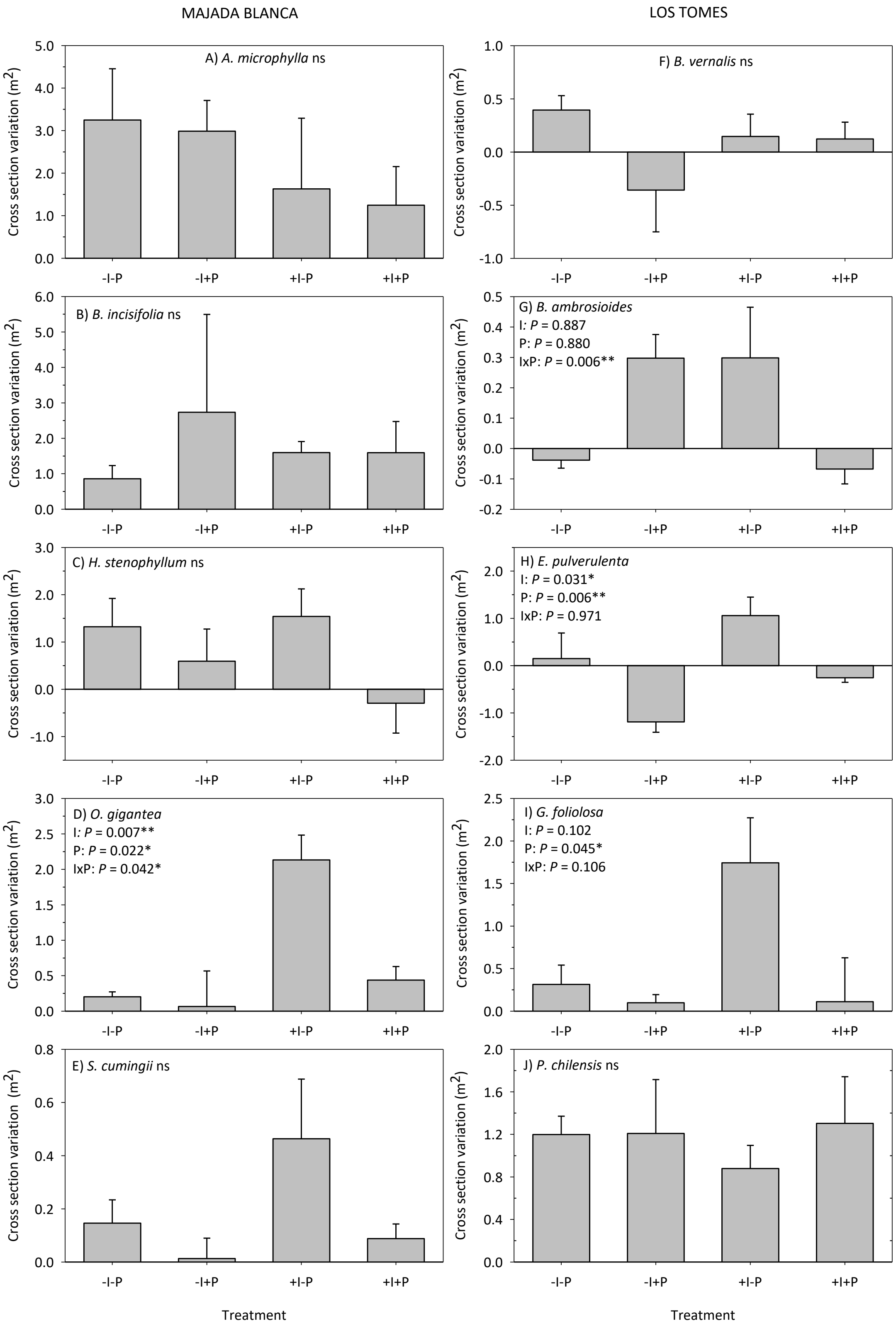

Figure 2. Net cross-section growth (mean + SE) for plants irrigated with fog water (+I) or pruned (+P), compared with control plants (–I–P). Detailed statistics are provided if significant effects were found for the treatments or for their interaction between the start and the end of the trial. ns: non-significant differences; *P* = probability; * *P* < 0.05, ** *P* < 0.01; X: interaction.

Crecimiento neto de la sección transversal (media + EE) para plantas regadas con agua de niebla (+I) o podadas (+P), en comparación con las plantas control (–I–P). Proporcionamos estadísticas detalladas cuando se detectaron efectos significativos para los tratamientos o para su interacción entre el inicio y el final del ensayo. ns: diferencias no significativas; *P* = probabilidad; * *P* < 0, 05, ** *P* < 0,01; X: interacción.

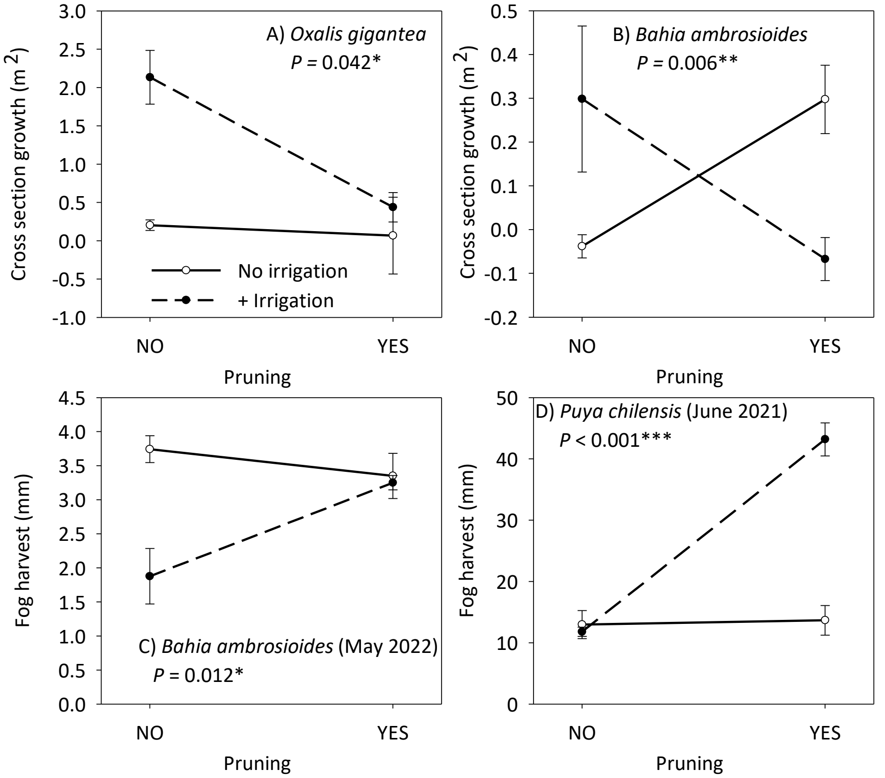

Figure 3. Interaction between irrigation and pruning in xerophytic species in two sites in the Coquimbo Region. Values are mean ± SE. P = probability for the interaction. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Interacción entre el riego y la poda en especies xerofíticas en dos sitios en la Región de Coquimbo. Los valores son medias ± EE. P = probabilidad para la interacción. * $P < 0,05$, ** $P < 0,01$, *** $P < 0,001$.

gure 2H). *Gochnatia foliolosa* (D. Don) D. Don ex Hook. & Arn. var. *foliolosa* also grew better without pruning (+I–P, Figure 2I).

Branch growth dynamics. Figures 4A-E show the net growth of tagged branches in Majada Blanca. *Adesmia microphylla* branch lengths (called primary branches) in control plants (–I–P) had the lowest net growth (*ca.* 4 cm) along the evaluated period (Figure 4A). The best treatment was no irrigation plus pruning (–I+P), although with similar values to +I–P and +I+P. Despite these trends, we did not find significant differences for the main effects or their interaction. Secondary branches that were cut in pruned plants (Cut–I, Cut+I treatments in Figures 4) barely grew during the experiment (*ca.* 1 cm), without significant effect of watering.

None of the treatments showed significant effects on *Bridgesia incisifolia* (Figure 4B). Irrigation treatment had significant effects on *H. stenophyllum*, being the +I+P treatment followed by +I–P those with the most positive effects on branch growth ($P = 0.014$) (Figure 4C).

On the other hand, *O. gigantea* growth was favored by +I–P, followed by +I+P (Figure 4D), an irrigation effect close to significance ($P = 0.069$). Finally, *S. cumingii* +I–P was the best treatment (Figure 4E). However, the only effect close to significance was pruning ($P = 0.061$), where this treatment was detrimental to branch growth. In addition, the secondary cut branches of irrigated plants exceeded those of nonirrigated plants, but not significantly. In Los Tomes, none of the treatments produced a significant influence (Figures 4F-J).

Effects of irrigation and pruning on fog harvest. Pruning negatively affected fog harvest in *A. microphylla* in Majada Blanca on six out of 17 evaluated dates, contrary to the expectations (Figure 5A). This is shown by the separation of the non-pruned treatments from those pruned. However, only the last three dates can be associated with this treatment, since this was applied after June 2021. In contrast, a positive effect of pruning was observed for *Bridgesia incisifolia* in August 2021 and May 2022 (Figure 5B).

Heliotropium stenophyllum was favored by irrigation in April 2021, as expected (Figure 5C). Conversely, irrigation impaired the performance of *O. gigantea* in four months (red, black treatments were above the blue, green treatments, Figure 5D). Finally, pruning and irrigation had negative effects in fog harvest by *S. cumingii* in July 2021, and August 2021-May 2022, respectively (Figure 5E).

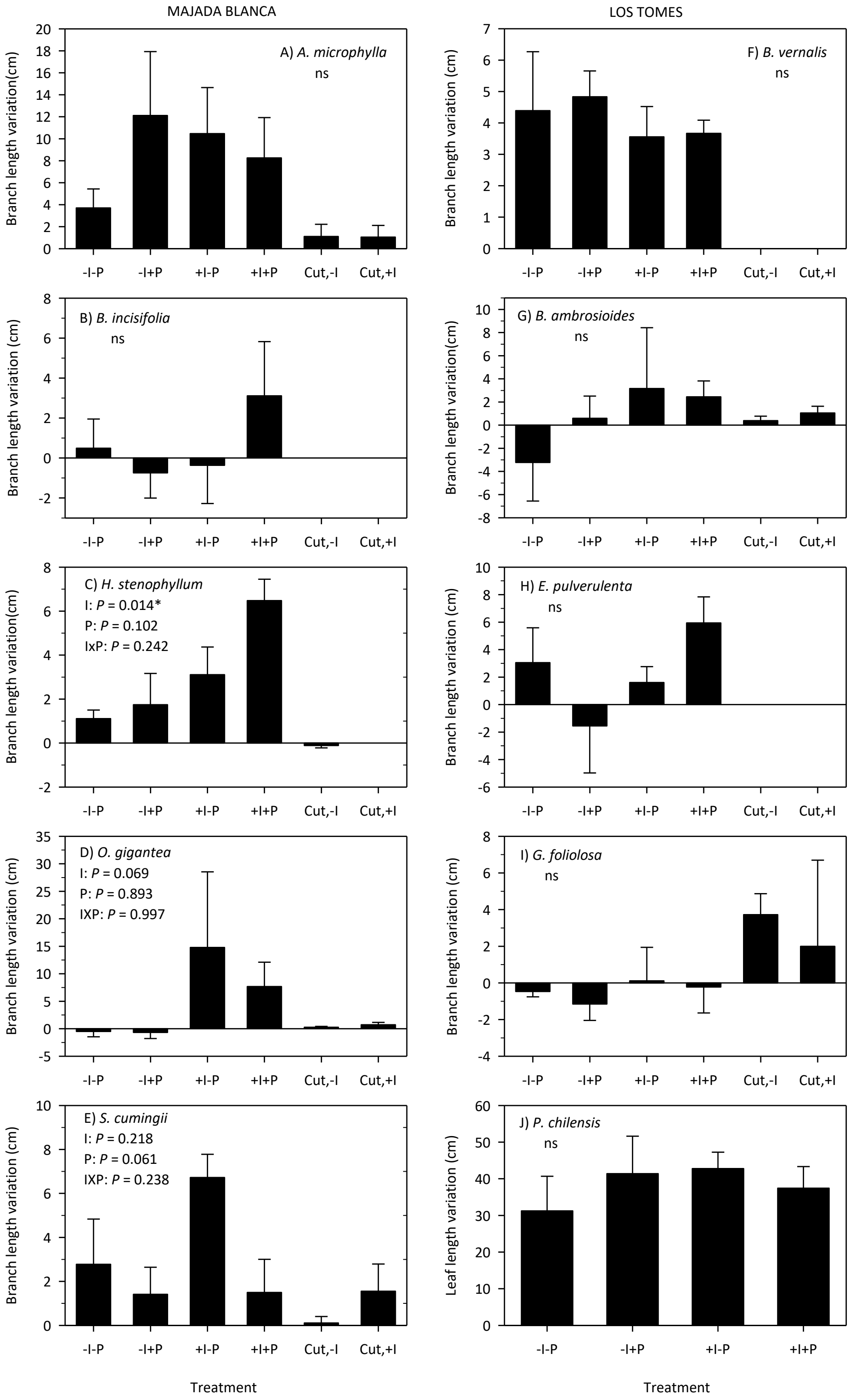

Figure 4. Net branch growth (mean + SE) for plants irrigated with fog water (+I) or pruned (+P), compared with control plants (–I–P). Cut,+I and Cut,–I refer to the secondary cut branches irrigated or non-irrigated, respectively (these treatments did not grow at all in some species); they were not selected for *P. chilensis*. Detailed statistics are provided when significant or near-significant differences were found for treatments between the start and end of the study. ns: non-significant differences; *P* = probability; * *P* < 0.05; X: interaction.

Crecimiento neto de las ramas (media + EE) de las plantas regadas con agua de niebla (+I) o podadas (+P), en comparación con las plantas control (–I–P). Cut,+I y Cut, –I se refieren a las ramas secundarias cortadas regadas o no regadas, respectivamente (estos tratamientos no crecieron en absoluto en algunas especies); no se seleccionaron para *P. chilensis*. Proporcionamos estadísticas detalladas cuando se detectaron diferencias significativas o casi significativas para los tratamientos entre el inicio y el final del ensayo. ns: diferencias no significativas; *P* = probabilidad; * *P* < 0,05; X: interacción.

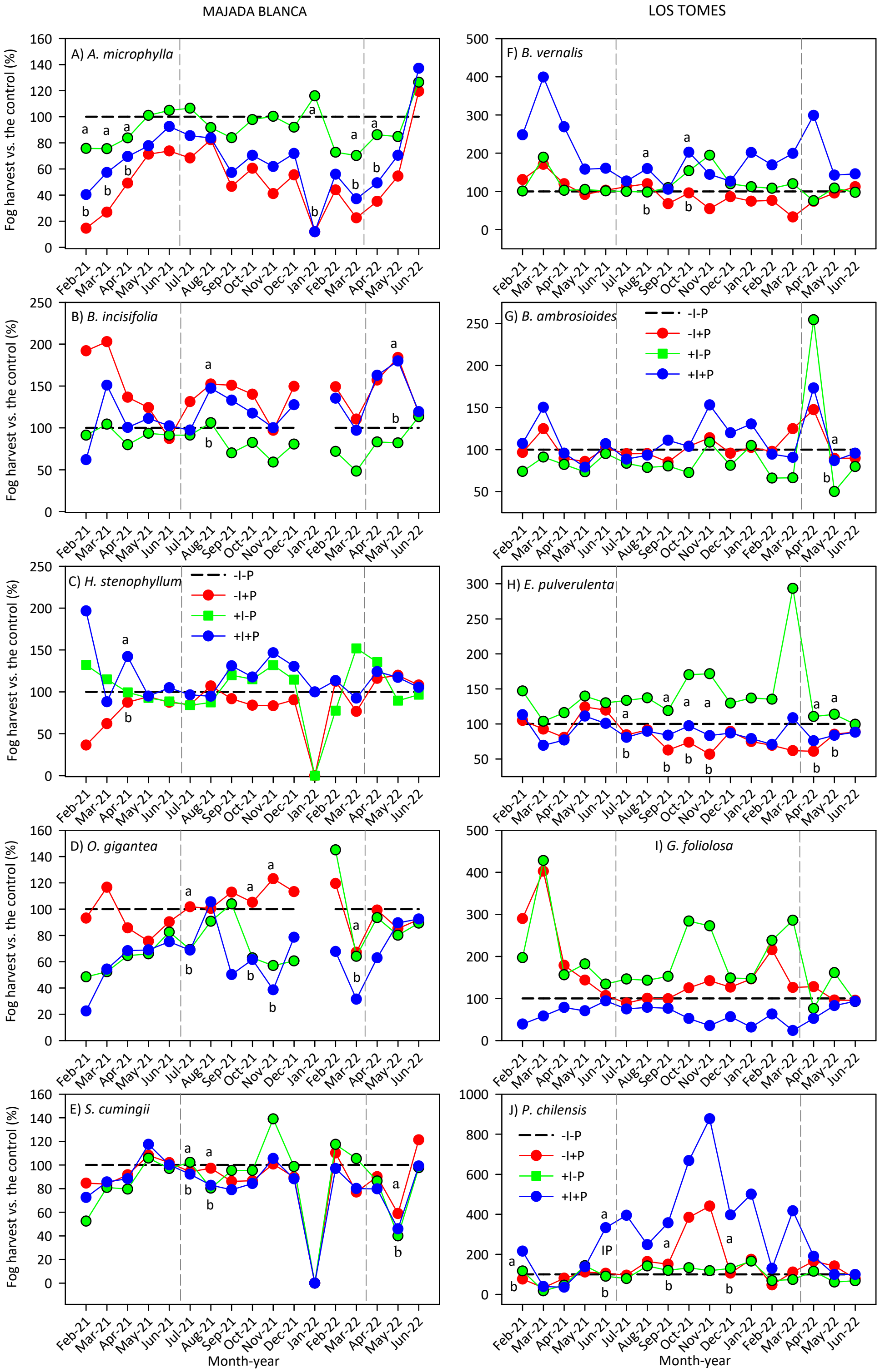

Figure 5. Time series of fog harvest for different species in the sites Majada Blanca and Los Tomes subjected to irrigation (+I) and pruning (+P) versus no irrigation (–I) and no pruning (–P). Fog harvest was expressed as a percentage of the control treatment (–I–P), which was always taken as 100%. Vertical dashed lines indicate the approximate dates of pruning. Different superscripts indicate significant differences among treatments for every date analyzed separately. On some dates there are no data points, because the control marked “zero collect”.

Series temporales de cosecha de niebla para diferentes especies en los sitios Majada Blanca y Los Tomes sometidas a riego (+I) y poda (+P) versus no riego (–I) y no poda (–P). La cosecha de niebla se expresó como porcentaje del tratamiento control (–I–P), que siempre se tomó como 100%. Las líneas discontinuas verticales indican las fechas aproximadas de poda. Diferentes superíndices indican diferencias significativas entre tratamientos para cada fecha analizada por separado. En algunas fechas no hay puntos de datos, porque el control marcó “cero recolección”.

Table 4. Summary of the patterns found in Figure 5.

Resumen de los patrones encontrados en la figura 5.

Site/species	Irrigation effect (number of months)	Pruning effect (number of months)	Irrigation x pruning interaction
Majada Blanca			
Adesmia microphylla		Negative (3)	
Bridgesia incisifolia		Positive (2)	
Heliotropium stenophyllum	Positive (1)		
Oxalis gigantea	Negative (4)		
Senna cumingii	Negative (2)	Negative (1)	
Summary Majada Blanca	7 effects/85 months = 8.2%	6 effects/85 months = 7.1%	
Los Tomes			
Baccharis vernalis	Positive (1)	Positive (1)	
Bahia ambrosioides	Negative (1)		Detected, see Figure 3C
Escallonia pulverulenta		Negative (6)	
Gochnatia foliolosa			
Puya chilensis	Positive (3)	Positive (2)	Detected, see Figure 3D
Summary Los Tomes	5 effects/85 months = 5.9%	9 effects/85 months = 10.6%	

At Los Tomes site, *Baccharis vernalis* responded positively to pruning in August 2021 and to irrigation in October 2021 (Figure 5F). Irrigation impaired fog harvest in *Bahia ambrosioides* only during May 2022 (Figure 5G). This effect occurred in the absence of pruning (Figure 3C). Fog harvest by *E. pulverulenta* was impaired by pruning during six months (Figure 5H). *Gochnatia foliolosa* did not show any effect of the main treatments (Figure 5I). Lastly, *P. chilensis* was influenced positively by irrigation in February, June, and December 2021; and positively by pruning in June and September 2021. The interaction effect on June 2021 is marked in Figure 5J by the acronym IP. On this date, there was a significant interaction at $P < 0.001$, due to a better fog harvest when pruning was applied under irrigated conditions only (Figure 3D).

In summary, we detected few significant effects for the experimental treatments: 12 effects of irrigation on both sites (5 positive and 7 negative); and 15 for pruning (5 positive and 10 negative) (Table 4). Los Tomes showed more positive effects of pruning or irrigation than Majada Blanca. These numbers represented a frequency of 7.1% of the total of evaluated months for irrigation (17 months x 10 species), and 8.8% for pruning.

When making statistical comparisons for the accumulated fog harvest in 17 months, *O. gigantea* showed a negative effect of irrigation ($P = 0.053$), consistent with the pattern observed monthly (Figure 5D). In Los Tomes, *P. chilensis* was favored by pruning on a cumulative basis ($P = 0.053$), agreeing with the effect of this intervention (but not for irrigation) on a monthly scale (Figure 5J).

DISCUSSION

Irrigation rates. There is limited information on the water requirements of wild species in xeric environments compared to agronomic species (Bown et al., 2018; Oros, 2022). Recent research in the semi-arid zone of Chile is using the Normalized Difference Vegetation Index and derived crop coefficients (Kc) to estimate actual evapotranspiration from potential evapotranspiration (Veas et al., 2017). Based on this approach with the FAO Penman-Monteith equation (Allen et al., 1998), we likely provided 55% of the water requirements of larger species, while the water requirements of smaller species were likely met (216–566%) in 2021 (Cuevas et al., unpublished data). In 2022, increased irrigation ensured all species received more than the 2021 natural water supply, likely meeting the needs of all species (92-141% for larger species vs. 540-942% for smaller species). However, this method, developed for fruit crops, may not fully apply to xerophytes, as Kc is expected to vary among species, and physiological data on water use (i.e., stomatal conductance) in many wild xerophytes is lacking. Additionally, many species are summer deciduous, with Kc values near zero during dry periods, rising only with rain or irrigation. These complexities suggest that water dynamics in xeric ecosystems depend heavily on species phenology and seasonal patterns, making generalizing based on agronomic models difficult.

Our irrigation treatment varied from 24 to 60 L plant^{-1} month^{-1}. This is significantly higher than the 8 to 28 L plant^{-1} month^{-1} reported in other studies on sclerophyllous or xerophytic plantations in the Coquimbo Region (Bown et al., 2018; Oros, 2022). This generalized approach is intended to meet the needs of species with higher water demands, recognizing that water availability is a critical limiting factor in xeric environments. However, the lack of species-specific adjustments likely introduces variability in plant responses, particularly in species adapted to low water inputs or drought tolerance mechanisms.

Response of the plant growth to irrigation. Only certain species showed a cross-sectional growth response to irrigation. While other species displayed trends suggesting potential long-term effects, the positive impact of irrigation is expected, as water availability activates dormant buds, enhancing budburst and biomass accumulation (Signorelli et al., 2022). This response is characteristic of xerophytes under water-limited conditions, where even small increases in water can rapidly trigger growth (Olivares & Squeo, 1999). Our results for *A. microphylla* differ from those observed in *A. confusa*, where irrigation increases biomass and diameter at the root collar (Oros, 2022). The lack of significant height differences across treatments in our study (data not shown) aligns with findings from Peña-Rojas et al. (2018) and Oros (2022), suggesting that height may not be as responsive to short-term management interventions.

Oxalis gigantea, *Bahia ambrosioides* (Figure 3B), and *E. pulverulenta* were the most responsive species in cross-section growth. Regarding branch elongation, irrigation favored *H. stenophyllum*, and *O. gigantea.* Most of these species have a shallow root system (Squeo et al., 1999; Menceyra et al., 2021; Table 3), which would allow for rapid uptake of water from precipitation or irrigation compared to deep-rooted species. There is no root data for several taxa (*Baccharis vernalis*, *E. pulverulenta*, *G. foliolosa*), but some other species with shallow roots did not respond to irrigation (*Bridgesia incisifolia*, *P. chilensis*). Similarly, Olivares & Squeo (1999) show that evergreen species are less affected by rain than deciduous species. In our research, plants responded to irrigation regardless of their growth habit (Table 3). These facts suggest the existence of other factors that control the response to irrigation.

Bridgesia incisifolia and *O. gigantea*, with their shallow roots, use water < 50 cm deep, probably recharged by rain, while *H. stenophyllum* and *S. cumingii*, with shallow and dimorphic roots, respectively, mostly use deeper water of different origins (Squeo et al., 1999). The proportion of deep water never drops below 82%, indicating that irrigation or rain only provide a smaller portion of the hydric plant budget in years of low precipitation (Torres et al., 2002). This phenomenon may have occurred in our experiment. Only in years with high pluviometry can species opportunistically use rainwater (Squeo et al., 1999). Consequently, Olivares & Squeo (1999) demonstrate enhanced growth response to precipitation of plant communities of the Coquimbo Region under adjacent years of contrasting rainfall (47 versus 233 mm).

The lowest dependence of plants on surface water (rain or irrigation) can also be related to the hydraulic lifting phenomenon. This is the passive redistribution of soil water by roots from deep layers to the driest layers near the soil surface (Muñoz et al., 2008). At least two of our species are hydraulic lifters: *S. cumingii*, and probably *A. microphylla* (based on the behavior of *A. bedwellii*). In addition to data for other species (Muñoz et al., 2008), this phenomenon is likely widespread in the semi-arid flora of the Coquimbo Region, especially for dimorphic root species.

Finally, the huge annual rainfall of 233 mm reported by Olivares & Squeo (1999) is equivalent to 142-1,461 liters year^{-1} (depending on the shrub area), while our irrigation of 288-720 liters year^{-1} can only mimic the rainfall effect in small species (< 1.2- < 3 m^2 cross-section). In fact, several of our responsive species were at or below 3 m^2, with a few exceptions. In addition, the rain falls more uniformly than irrigation concentrated in just two 10 cm diameter wet bulbs, regardless of leaf interception. This background may explain why our irrigation program, although more intensive than most in the region, has never been able to match the effect of a large rainfall.

Response of plant growth to pruning. Previous studies in similar ecosystems show that pruning can have a significant positive impact on tree growth (Azócar et al., 2001; Vita & Hernández, 2004). Conversely, in our study, pruning reduced cross-sectional growth in three species, likely due to the immediate loss of photosynthetically active tissues and the reduced capacity for regrowth. The contrasting patterns may be a consequence of precipitation magnitude, as the first study is conducted under 150-328 mm year^{-1}, while the second corresponds to a cloud forest that receives 419 mm year^{-1} of rain and fog (Barbosa et al., 2010). In fact, Azócar et al. (2001) note that under 100 mm of rainfall, plant mortality is high for the more severe pruning. Drawing a parallel with browsing, Schulte (2014) asserts that a large proportion of plant species respond inconsistently to grazing, tending to decrease their performance when environmental conditions are suboptimal, such as during a drought grazing period.

Branch length, with a negative or null effect of pruning, responded similarly to cross-sectional growth. The previous background suggests that the removal of the branches weakens the plant's ability to allocate resources effectively for recovery. In another study in the Coquimbo Region, Schulte (2014) shows that palatable species perform better in unbrowsed areas, while the effect is quickly lost with less palatable species. Under a precipitation of 40-115 mm year^{-1}, only a few cases show the opposite trend, and finally, some species are indifferent to the browsing. In either case, an excluded plant is more likely to grow better than a browsed plant, because herbivores will continue to disturb the latter. This is analogous to frequent pruning. After a period without disturbance, the browsed individuals should recover.

Notably, interactions between irrigation and pruning were significant in two cases, with irrigated, non-pruned plants exhibiting better growth. These findings underscore the need to consider both treatments together, as their combined effects are not simply additive but interact in ways that vary between species. The differential responses observed suggest that xerophytic plants in fog ecosystems require careful management that integrates both water availability and structural maintenance for optimal growth and fog capture.

Regarding pruned branches, they have limited potential to recover, similar to browsed plants. The disparity between primary and secondary branches likely stems from the intact branches maintaining metabolic activity, whereas cut stems must repair damaged tissues and activate dormant buds. Bhatla (2003) also states that after this intervention the hormonal relationship becomes unbalanced in favor of cytokinins and gibberellins that will promote cellular development from the cambium meristem, affecting the basal buds and promoting the formation of biomass. Lateral buds typically do not develop until the following spring after vegetative dormancy (Pallardi, 2008). This delay in response, coupled with the systemic signaling triggered by herbivory, as Waterman et al. (2019) note, implies that pruning does not immediately elicit a localized recovery response.

Fog harvest response to plant irrigation and pruning. Few significant effects were observed in our experimental setup, with only 13 out of 170 instances (7.6%) showing significance in Majada Blanca, mostly negative. Los Tomes exhibited similar proportions, but with more positive effects. Notably, individual species exhibited consistent responses to irrigation and pruning, without mixed effects across different dates, suggesting a species-specific response. *Oxalis gigantea*, for instance, showed a dense lichen coverage before irrigation (Figure 1B), which likely restricts fog drip as lichens absorb water (Stanton et al., 2014). After irrigation, *O. gigantea* showed notable recovery, increasing leaf production, cross-sectional area, branch length, alongside a reduction in lichen coverage. As previously mentioned, *O. gigantea* possesses a shallow root system that is simultaneously succulent (Squeo et al., 1999), enabling this species to utilize partially rainwater or irrigation and to store water belowground. Notwithstanding the presence of these functional traits, fog drips did not increase as expected, likely because the newly formed leaves intercept and retain fog, preventing direct water drip (Cuevas et al., 2003b). Other species, such as *H. stenophyllum* and *P. chilensis*, which showed fewer architectural alterations in response to the various treatments applied, exhibited a larger fog drip response to irrigation, supporting the idea of species-specific responses.

Pruning generally resulted in negative effects, reducing fog drip by decreasing aboveground biomass. However, in *P. chilensis* (Bromeliaceae), the unique rosette growth form led to rapid recovery post-pruning, making it the species with the fastest aboveground biomass recovery (Figure 4J). This was accompanied by consistently high fog accumulation beneath its canopy, verified through repeated field checks to ensure accuracy. This suggests that *P. chilensis*' growth form may allow for a positive response to both irrigation and pruning, unlike most other species.

In some cases, pruning under irrigated conditions enhanced fog harvest, likely because the formation of new leaves—which requires water— mediated fog capture. Without irrigation, pruning generally reduces fog collection, likely due to biomass loss. Moreover, the reduction in plant size due to pruning is directly associated with a decrease in total fog harvest, as fog collection is proportional to the plant's surface and cross-sectional area (Ingraham & Matthews, 1988). Given that pruning consistently had a negative impact on both growth and fog collection, our results suggest that intense herbivory impair the ecosystem's fog-harvesting function by removing branches and leaves that are slow to recover.

Overall, responses to treatments were less pronounced than expected. Previous studies (Cuevas et al., 2003a) identify height and volume as strong predictors of fog harvest in these species, but the modest growth response we observed may have limited treatment effects. Regarding the implications of our findings for vegetation management, several international-level management protocols, as well as protocols specific to central Chilean vegetation, emphasize the importance of pruning in maintaining the hydric balance of trees in climate change scenarios (Kozlowski & Davies, 1975; Forrester et al., 2012; Ye et al., 2021; Cruz et al., 2021). However, when applied to specific settings, these protocols generally fail to request evidence of intervention effectiveness, let alone consider the importance of varying rainfall regimes and fog capture across many regions (e.g., Ministerio de Agricultura, 1998; CONAF, 2025). Therefore, it is important to evaluate the effects of interventions experimentally.

CONCLUSIONS

Our hypothesis that enhanced plant growth from irrigation and pruning would lead to increased fog harvest is partially supported, revealing no consistent patterns among the analyzed species. The growth response of xerophytic plants is species-specific; generally, irrigation has positive effects while pruning has negative consequences. Pruning reduces fog harvest in most cases, although some exceptions exist. Irrigated plants display varying capacities for fog collection, depending on the species. Prior to interventions, such as irrigation, individual species responses must be evaluated. A general conclusion is that irrigation positively stimulates growth, benefiting productive plantations and restoration efforts. In contrast, pruning often impairs short-term growth and should be minimized. Additionally, intense herbivory can detrimentally affect both growth potential and fog collection capacity. The findings of this study indicate that the impact of pruning is only evident in years with high precipitation levels or during treatments involving irrigation. Given that the plant community has adapted to the local soil conditions, which are relatively poor, and that some species responded while others did not, the present findings indicate the existence of a potential response and highlight the complexity of species-specific responses in these fog ecosystems.

AUTHOR CONTRIBUTIONS

JC was responsible for the experimental design and analysis of the results. EO contributed to the study design and revision of the final draft. PH provided equipment and site location. CB oversaw the field data collection, and RA contributed to the discussion and interpretation of the results. The preparation of the manuscript was carried out by JC, EO, PH, and RA.

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