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Population dynamics and orientation of the central Andean cushion *Azorella compacta*

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Running Title: *Azorella compacta* growth

Abstract

Azorella compacta (*llareta*; Apiaceae), a large woody cushion plant, is a remarkable species forming dense cushions and characterizing the high elevation rocky slopes of the central Andean Altiplano. Field studies of an elevational gradient of *A. compacta* within Lauca National Park in northern Chile found a reverse J-shape distribution of size classes of individuals with abundant small plants at all elevations. A new elevational limit for *A. compacta* was found at 5250 m. A series of cushions marked 14 years earlier showed either slight shrinkage or small degrees of growth up to 2.2 cm yr^{-1}. Despite their irregularity in growth, cushions of *A. compacta* show a strong orientation, centered on a north-facing aspect and angle of about 20° from horizontal. This exposure to maximize solar irradiance closely matches previous observations of a population favoring north-facing slopes at a similar angle. Populations of *A. compacta* appear to be stable, or even expanding, with young plants abundant and recolonization of disturbed habitats.

Key words: Andes, Parque Nacional Lauca, cushion plant, puna, growth rate

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INTRODUCTION

Azorella compacta (Apiaceae), a large woody cushion plant, forms an iconic species of the Altiplano Plateau of northern Chile, Bolivia, Argentina and Peru (Kleier & Rundel 2004). Known locally as *llareta*, it forms broad irregular cushions that commonly reach diameters of 3–4 m, or much more, on rocky slopes at high elevations. Its range extends across the Altiplano Plateau of the south-central Andes from southern Peru through western Bolivia and into the northeastern Chile and north-western Argentina (Martinez 1993). The species only rarely occurs below 4000 m and an upper elevational limit of 5200 m has been reported (Halloy 2002), making it one of the highest occurring woody plant species in the world.

Azorella compacta forms unusual bright green woody mounds on steep rocky slopes where few other plants survive (Fig 1a). Its surface consists of thousands of small stems that grow so tightly together that the plants have the consistency of smooth, green wood (Fig. 1b). While there are other cushion plants that have a similar growth form in the Andes and other parts of the world such as New Zealand, there are none that grow as large. Individual *A. compacta*, perhaps in some cases resulting from the merger of several individuals, can form an irregular but continuous cushion up to 10 m or more across. Previous research on *A. compacta* has described microhabitat selection, population structure, germination rate, and growth rate of the plants (Kleier & Rundel 2004), as well as the ecophysiology and energy balance of the *A. compacta* cushions (Kleier & Rundel 2009). There have also been concerns about conservation of the species due to past major harvesting of llareta for fuel in the early and mid-20th century, and *A. compacta* continues to be classified as a "data deficient" species (IUCN 2012).

The present research continues a long-term study of *A. compacta* begun in 1998, and expands existing data for growth rates in these cushions by revisiting plants marked 14 years earlier. A second objective was to broaden a community survey to better understand patterns in population structure by sampling an elevation gradient of *A. compacta* populations extending from elevations of 4400-5250 m. Finally, previous investigations on the significance of energy balance in cushion establishment (Kleier & Rundel 2009) were expanded to look at aspects of orientation and solar irradiance in mature cushions.

METHODS

Site description

Field studies were carried out in Lauca National Park, a protected area located 145 km east of the coastal city of Arica and adjacent to both Peru and Bolivia. The park covers 1379 km^2 of land classified as the central Andean dry puna (McGinley 2009), with elevations ranging from 3220-6342 m. A UNESCO World Heritage site, the park is renowned for high-altitude lakes Chungará and Cotacotani, a rich diversity of wildlife and flora, a spectacular backdrop of high volcanoes, and the small village of Parinacota with its 17th century church (Rundel & Palma 2000). The broad Altiplano Plateau in Lauca National Park lies largely at elevations of 4400-4900 m elevation, but with higher volcanic slopes which are home to extensive populations of *Azorella*.

The Andean Cordillera in the study region consists of folded and faulted Cretaceous and Tertiary sediments mixed with former volcanic centers of activity. Highway 11 crossing Lauca National Park reaches as high as 4600 m before dropping to 4500 m at Lago Chungará. Much of the substrate geology in the study region is formed by a chain of deeply eroded Miocene volcanoes, which make up the western margin of the Lauca Basin, and which are sometimes termed the Chilean Western Cordillera. The most prominent peaks are the Nevados de Putre (5775 m) and Cerro Belén, Cerro Tallacollo, Cerro Orotunco, and Cerro de Anocarire all of which reach above 5000 m. Several relatively young volcanic cones rise above the Altiplano plateau, including the Parinacota (6342 m), Ponerape (6240 m), and Guallatire (6063 m) within Lauca National Park (Rundel and Palma 2000).

Demography and elevational range

To assess elevational gradients in population structure, we measured 406 cushions sampled in 30 separate 100-m line transects established on rocky slopes with *A. compacta* populations throughout Lauca National Park. The lowest elevation transect was at 4247 m and the highest at 5182 m. The line intercept of each *A. compacta* cushion along these transects was recorded to the nearest cm. Each cushion was measured along two orthogonal axes, roughly corresponding to the greatest width and length, to provide a squared estimate of surface area (Kleier & Rundel 2004). The tape measure was allowed to follow the surface of the plant to account for irregular planar features. This was necessary as some plants have more undulations within them than others. GPS measurements were made to record the latitude, longitude, and elevation at the beginning point of each transect.

Elevational transects were extended on two different peaks, an unnamed peak that Corporación Nacional Forestal de Chile (CONAF) rangers called Cerro Apacheta Choquelimpie (5289 m) and Cerro Larancaugua (5447 m), to visually search for the highest occurring individual of llareta. Access was restricted by heavy snow and ice cover and avalanche risk to two higher peaks, Volcán Parinacota and Volcán Pomerape.

Determination of growth rate

The growth rate of *A. compacta* was determined by changes in dimensions of marked individuals that were first tagged in 1998, measured again in 2000 (Kleier and Rundel 2004), and resampled in January 2012. These plants are located approximately 2.5 km northwest of the village of Parinacota along the path to Lagunas Cotacotani (18° 12.554' S and 69° 16.132' W) at an elevation of 4454 m. Although 100 plants in four separate plots were originally marked, only 9 of the marked plants within one plot were able to be relocated. Presumably, *A. compacta* completely grew over at least some of the permanent tags of the remaining plants). However, one plot of tags was removed between 1998 and 2000, and it is likely that more were removed between 2000 and 2012, due in part to controversies regarding ownership and control of park land. In 1998, park staff indicated that the proposed plots would be located on public land. However, in 2012, we found several painted messages denoting the area as private property. While removal of the tags lessened the value of data gained from the plots, it indicates underlying desires of local Amayara populations to own and protect the park's resources. Notably, we found no signs of recent llareta harvesting in this area.

For the nine remaining tagged plants, we measured length and width in orthogonal axes across the apex of the cushion, perimeter, and height, which was determined from the apex of the cushion to the nearest western edge. We also noted any dieback (increase in dead tissue) and the presence of flowers or fruits.

Statistical analysis

For demography data, we used SPSS version 19 (IBM, USA). We used Pearson Correlation to determine if there were more plants at higher elevations and to determine if plants were smaller at higher elevation. Because we only had nine individuals to assess a long term growth rate, we used bootstrap analysis in R to expand the variation to a hypothetical population of 10,000 plants and assessed 95% confidence intervals of growth around the mean and median.

Cushion orientation

The aspect and the angle from horizontal that maximized the projected area of individual *A. compacta* cushions were determined visually with a compass and clinometer. After an isolated cushion was identified in a flat area without significant influence from local terrain, a raster-like approach was used. The assistant stood approximately 2 m from the individual cushion at a low angle (crouching) and walked in an arc around the plant, visually gauging the projected area at different aspects. When an aspect had been determined that maximized the projected area of the cushion at the low angle, the angle was increased (the assistant stood at an increased height off the ground), and the process was repeated until a maximum projected area was determined for all aspects and angles. A transect line was then used to connect the center of the individual cushion to the point in space that maximized the visual projected area of the cushion and the aspect of that transect line and the angle from horizontal was measured (Fig. 2). The same field assistant was employed for all measurements to avoid changes in bias between individual measurements. The declination from magnetic north of 5.33° W was determined for latitude 18°12'6.70" S, longitude 69°16'5.16" W for January 6, 2012 using the online NOAA Estimated Value of Magnetic Declination Calculator <http://www.ngdc.noaa.gov/geomag-web/#declination>.

RESULTS AND DISCUSSION

Demography and elevational distribution

A histogram demonstrates that the smallest size classes of *A. compacta* are most common at all elevational ranges (Fig. 3). This trend is the same when plants were measured using perimeter, instead of area. The mean canopy area for the 406 cushions measured, calculated as length x width, was 29 m^2 (± 2.10 SEM). A Pearson correlation analysis found a slight ($r = 0.129$), but significant ($p = 0.009$), negative relationship between elevation and size of plants. However, much of this pattern is due to the presence of a number of very large plants in transects sampled above 5000 m. The number of plants per 100-m transect ranged from 6 to 24, with a mean of 13.5 plants, and the number of plants per transect did not significantly correlate with elevation.

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Our field measurements included a new high altitude record for llareta, sampling *A. compacta* at an elevation of 5250 m, 50 m higher than previously reported (Halloy 2002). The species almost certainly grows at even higher altitudes on the slopes we surveyed, but a deep snowpack at the time of sampling restricted access.

Growth rate

The changes in perimeter over 14 years for the nine plants that were tagged in 1998 are shown in Table 1 and Fig. 4. A bootstrap analysis to determine a 95% confidence interval of growth rate around the mean and the median based on 10,000 replicates found a range from -2.86 cm yr^{-1} to 0.55 cm yr^{-1}. The negative growth rates resulted from a decrease in the individual perimeter over the sample interval. When the median was used for bootstrapping, the 95% confidence intervals around perimeter growth ranged -2.55 cm yr^{-1} to 2.09 cm yr^{-1}. These changes in perimeter corresponded to a radial growth rate of -0.5 to 0.4 cm yr^{-1}.

Despite these slow rates of mean growth, we also found that individual *A. compacta* can grow significantly more quickly under some conditions. As an example of rapid growth, we observed a semi-rectangular individual 20 cm by 40 cm, with a perimeter of 110 cm growing in a ditch on the side of the Highway 11 (Fig. 5). The ditch was presumably created when the highway was repaved in 1996. Thus, this individual is at most 16 years old and would have a minimum estimated growth in perimeter of 6.88 cm per year. It is possible that young *A. compacta* may grow more quickly in a planar fashion, while older plants allocate more growth to vertical changes in surface are; thus, increased water availability due to runoff may allow for increased growth rates.

Orientation of growth

Despite their seemingly irregular surface, the orientation of *A. compacta* cushions showed strong patterns favoring the maximum exposure of cushion surface area to annual solar radiation. The mean aspect of this orientation was to the north, with 60% of the plants sampled having a maximum exposure facing -30 to 30^{o} from true north. No plants had a maximum exposure of surface area that was more than 90^{o} from north (Fig. 6). The angle of maximum exposure similarly showed a marked orientation with a mean inclination of about 20^{o} from horizontal. Almost 60% of cushions has an angle between 16-30^{o} (Kleier & Rundel, 2009).

This orientation of exposure and inclination not only maximizes solar irradiance over the course of the year, but smoothes out much of the seasonal swings in irradiance that occur on a normal surface. Although and equivalent angle of inclination with a south-facing exposure would add up to 20% greater irradiance in summer, this orientation would receive less than half of the winter irradiance received by the north-facing exposure.

GROWTH AND POPULATION DYNAMICS

The large area of many *A. compacta* cushions is not unique within this interesting genus. Continuous mats of *Azorella selago* on the subantarctic Marion Island can be tens of meters across (Huntley 1972), although these broad mats have been shown to often consist of multiple individuals grown together (Mortimer et al. 2008). A similar pattern of merged canopies is likely present in *A. compacta*. For *A. selago*, smaller round cushions are found growing at all angles to the slope, but as cushions become larger and more elongated, growth is oriented vertically perpendicular to the plain of steeper slopes (Boelhouwers et al. 2000). *Azorella monantha* in the central Andes of Argentina occur as broad carpets that grow over all manner of objects including rocks, debris and other plants (Méndez 2011).

Population structure in *A. compacta* follows the same trend of a reverse J-shaped curve of population distribution that was noted in 2000, with many smaller plants in what appears to be a pre-reproductive stage, i.e. < 2 m perimeter (Kleier & Rundel 2004), and this pattern is repeated at all elevations including those growing above 5000 m. This population structure suggests that there is some degree of regular success in the establishment of cushion seedlings. There are clearly tradeoffs between seedling establishment and life span in many alpine plants, but many cushion plants seem able to maintain such success as well as great longevity. Similar population structures have been reported for *Azorella madreporica* in the high Andes of central Chile (Fajardo et al. 2008), *A. selago* in the subantarctic Indian Ocean (le Roux & McGeoch 2004), and in the closely related *Llaretia acaulis* in the Andes of central Chile (Armesto et al. 1980). Similarly, cushions of *Eritrichium nanum* in the Austrian Alps exhibit a reverse J-shaped curve of population distribution (Zoller & Lenzin 2004). Other high elevation woody species have been shown to exhibit similar trends of a reverse J-shaped population structure. The dwarf tree *Polylepis tarapacana* (Rosaceae) that co-occurs with *A. compacta* has a similar size class distribution with many young plants across a similar elevational gradient (Hoch & Körner, 2005).

Such size-age structure can be readily maintained by episodic but frequent seedling recruitment, followed by relatively low rates of mortality once these seedlings are established (Doak & Morris 2010). Poor recruitment of seedlings in the temperate alpine cushions *Minuartia obtusiloba* and *Paronychia pulvinata* is balanced by an estimated longevity of 200 and 324 years, respectively (Forbis & Doak 2004). Similarly, the alpine cushion *Silene acaulis* in the Pyrenees Mountains has irregular seedling establishment but life spans in excess of 300 years (Morris & Doak 1998, García et al. 2002).

Our findings of slow or even negative growth rates for *A. compacta* are supported by our previous research which reported very low rates of radial growth. We previously reported a mean radial growth rate of 1.46 cm yr^{-1} over 14 months (Kleier & Rundel 2004). The large size and slow rates of growth established for *Azorella* clearly indicate a great age of centuries or more for the larger cushions. The current studies of growth averaged over 14 years have shown slow but variable rate of radial growth from shrinkage, despite the woody structure of the cushion, to about 0.4 cm yr^{-1}, although it is based on a small sample size. Salguero-Gómez and Casper (2010) illustrate the need to keep plant shrinkage in demographic models.

Other studies have suggested even lower growth rates for *A. compacta*. Ralph (1978) reported annual radial growth averaging about 1.4 mm yr^{-1}. Halloy (2002) reported average radial growth of 1.55 mm yr^{-1}, but also found that individual plants could grow at rates up to 12.3 mm yr^{-1}, consistent with our observations of faster growth in young plants. Radial growth rates for cushions of *A. monantha* in the central Andes of Argentina are 1.15-190 cm per year (Méndez 2011), while *A. selago* on sub-Antarctic Marion Island ranged from an average of 0.28 cm per year (Frenot et al. 1993) to 0.426 cm per year (le Roux & McGeoch 2004).

Growth in *A. compacta* is seasonal (Halloy 2002), reflecting the highly seasonal summer precipitation regime of its habitat. Although the Altiplano climate regime presents favorable daytime temperatures for growth throughout the year, two-thirds of the annual precipitation falls in January and February, with a long dry season from April through November that accounts for only 4% of the total.

Slow rates of radial growth have been reported in other alpine cushion plants. *Silene acaulis* in the Rocky Mountains which has been reported to have a radial growth rate of 1.0-1.5 cm yr^{-1}

(Benedict 1989), and the arctic cushion *Diapensia lapponica* has a mean radial growth rate of only 0.6 mm yr^{-1} (Molau 1996).

Our study also indicated that the way plants are measured changes overall growth rate substantially. Several authors have noted that growth in *A. monantha* mats is not equal rates in all directions (Halloy 2002, Méndez 2011), supporting our concerns about the manner in which growth rates should be measured. Unlike growth measurements of the temperate cushion *Silene acaulis* (Morris & Doak 1998), *A. compacta* cannot be measured in simple terms of radial growth because this omits volume of the plant. Likewise, growth measurements of the congener, *A. selago*, were analyzed by using height (le Roux & McGeoch 2004), but that is not possible with *A. compacta* because the cushion is too dense and often forms over small boulders. To take a height measurement, a hole would have to be drilled through the plant. As *A. compacta* contains more three-dimensional volume than most cushion plants, further ontogenetic models are necessary to determine more robust growth rates.

Azorella compacta was found up to an elevation of 5250 m in our study, which is higher than the previously recorded elevation by Halloy (2002). The individual found at this elevation was not flowering and was of a size < 2 m perimeter that may not be reproductive (Kleier & Rundel 2004). We did not note a significant trend in smaller cushions with increasing elevation, and thus failing to provide evidence of plants at higher elevations in response to climate change (Lenoir et al. 2008). A change in morphology to shorter and broader canopy architecture with increasing elevation has been noted for co-occurring high elevation trees of *Polylepis tarapacana* (Macek et al. 2009).

ORIENTATION

Microsite selection by *A. compacta* strongly favors establishment at the base a moderate to large-sized boulders, and preferentially on the north-facing side (Kleier & Rundel 2004). Nowhere in our surveys have we observed individuals growing in sandy soils without boulders present. One potential advantage of such positions would be that heat storage in boulders could provide some benefit to adjacent seedlings in buffering diurnal changes in soil temperature (Poesen & Lavee 1994). Positions adjacent to boulders may also offer favorable conditions of water availability in arid and semi-arid regions. Boulders can influence surrounding hydrology by collecting surface flow, slowing evaporation caused by soil warming, and condensing moisture in the evening at the rock/soil interface (Flint & Childs 1984; Nobel et al. 1992; Poesen & Lavee 1994).

However, the strong and significant correlation of establishment on the north side of boulders (Kleier & Rundel 2004) suggested that energy balance may be a more significant factor in microhabitat selection. *Azorella compacta* cushions, despite their irregular form, strongly favor maximizing exposure of surface area to solar radiation. Cushions are oriented to favor an exposure to the north at angle centered on about 20^{o} from horizontal. This orientation at 18^{o}S, well within the Tropic of Capricorn, favors solar radiation input. This conclusion was reinforced by Kleier and Rundel (2009) who demonstrated the significance of slope exposure and azimuth as components of seasonal patterns of irradiance. Models of total daily solar irradiance over a seasonal cycle showed that north-facing slopes at a slope angle of 20^{o}, very close to the favored slope angle for *Azorella* establishment (Kleier & Rundel 2009), received more annual irradiance than those on horizontal or south-facing slopes of the same angle.

CONCLUSIONS

Although populations of *A. compacta* appear to have rebounded well since heavy harvesting of the cushions for fuel in the early and middle parts of the last century, growth rates of individual plants are clearly very slow. Low growth rates for *A. compacta* led Alliende and Hoffman (1983) to consider that the species could become threatened under conditions of continued harvesting for fuel. Likewise, Benoit (1989) concluded that the species is vulnerable in Chile. However, we have observed large reproductive populations of *A. compacta* across Lauca National Park, and little evidence of significant harvesting. At least in this area, the future survival of *A. compacta* does not appear to be under significant threats from direct human interactions. However, global change may present some level of unknown threat as Andean communities are pushed to higher elevations. Global change modes predict a 3 to 4 °C rise in temperatures in the central Andes (Anderson et al. 2011), which might well shift elevational distributions several hundred meters higher.

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Table 1. Representing measured perimeters of individual *Azorella compacta* in 1998 and resampled in 2012.

Individual	1998 perimeter (m)	2012 perimeter (m)	Change in perimeter (m)
1	0.78	0.88	0.1
2	4.3	4.23	-0.07
3	6.13	5.23	-0.9
4	1.15	1.11	-0.04
5	3.61	3.92	0.31
6	5.12	5.37	0.25
7	4.47	4.3	-0.17
8	8.64	8.25	-0.39
9	5.51	4.94	-0.57
Average ± SD	4.41 ± 2.42	4.25 ± 2.24	-0.16 ± 0.39

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Figure 1. *Azorella compacta.*a) irregular cushion form of growth; b) surface of male cushion.

Figure 2. Sampling design for measuring cushion angle and azimuth of orientation.

Figure 3. Relative proportion of cushion sizes in three groups of elevational populations of *Azorella compacta*.

Figure 4. Comparison of surface area, calculated as length x width, for *Azorella compacta* in 1998 (closed circles) and 2012 (open circles); n =9.

Figure 5. *Azorella compacta* growing in a ditch alongside Highway 11, which connects La Paz, Bolivia and Arica, Chile. The highway was paved in 1996, presumably when the curb was constructed, and thus this plant is at most 16 years old. Photo was taken January 5, 2012.

Figure 6. Relative distribution of orientation by cushions of *Azorella compacta*: a) orientation by aspect; b) orientation by angle from horizontal.

Figure 1a.

Figure 1b.

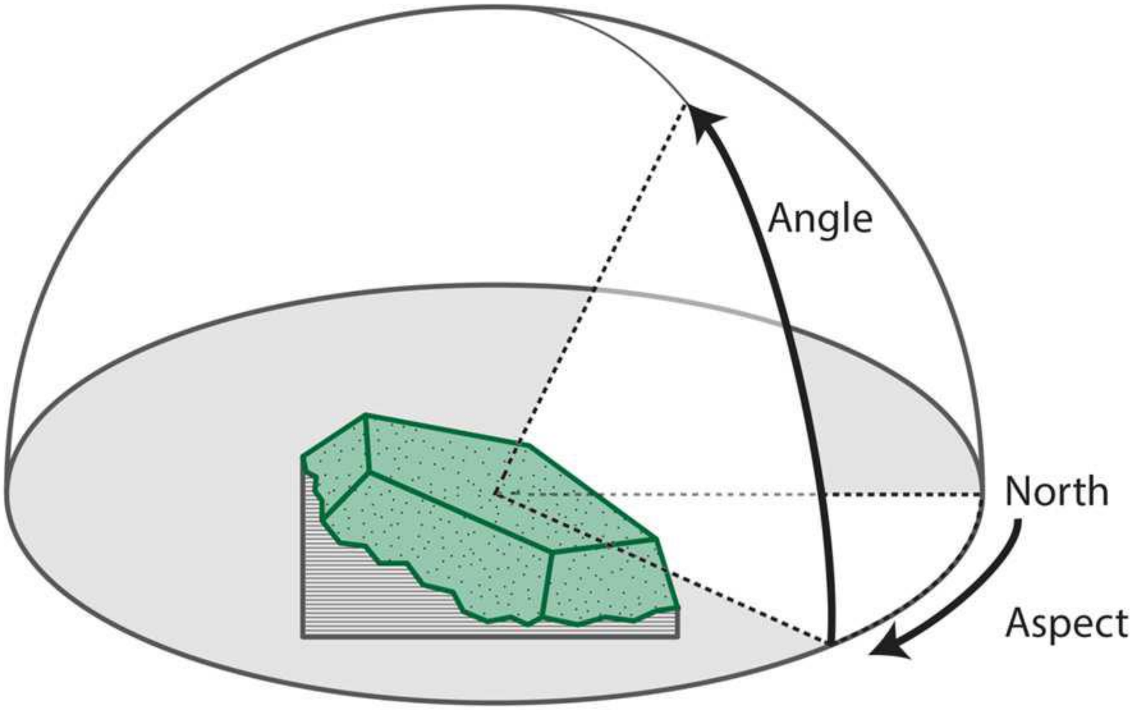

Figure 2.

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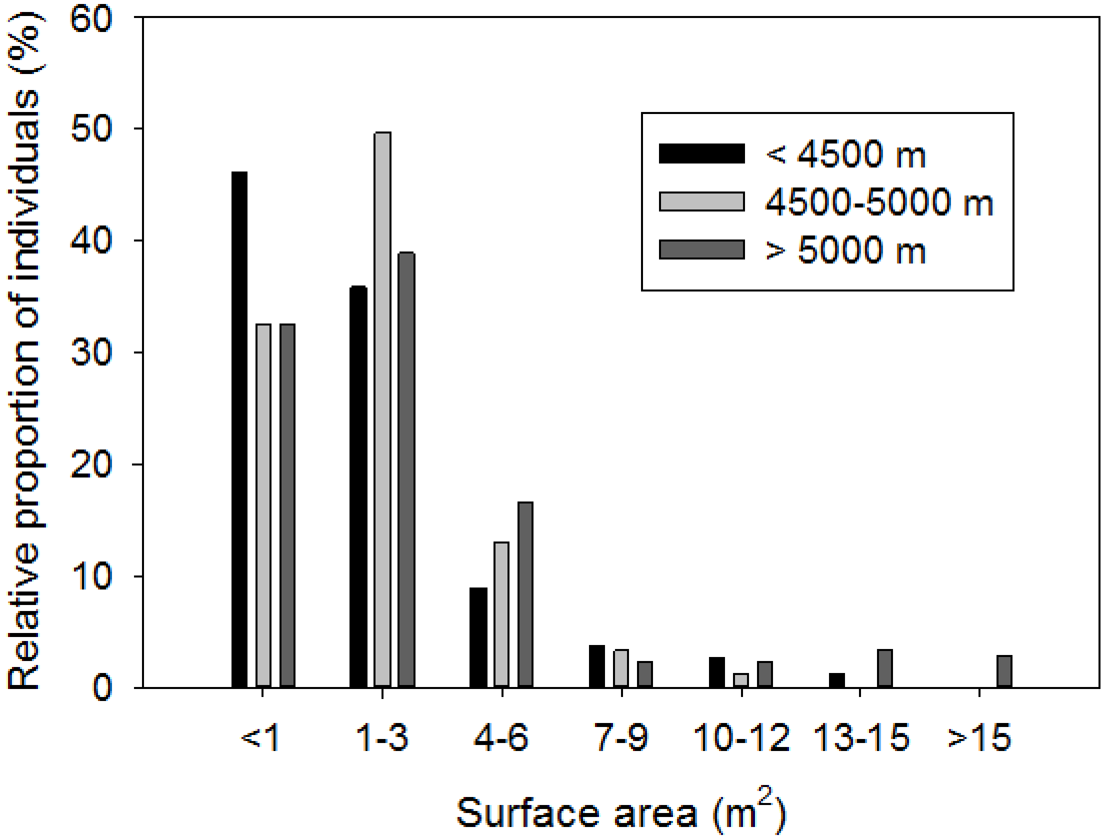

Figure 3.

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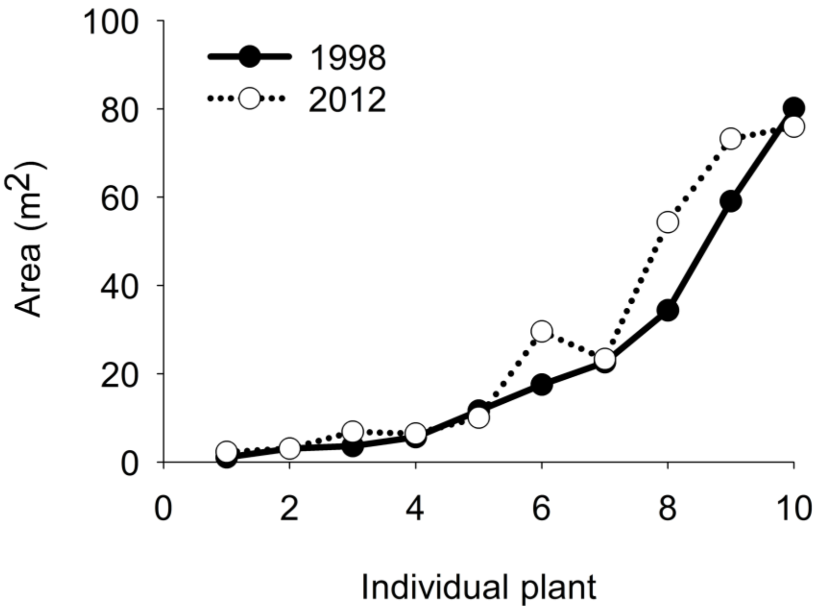

Figure 4.

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Figure 5.

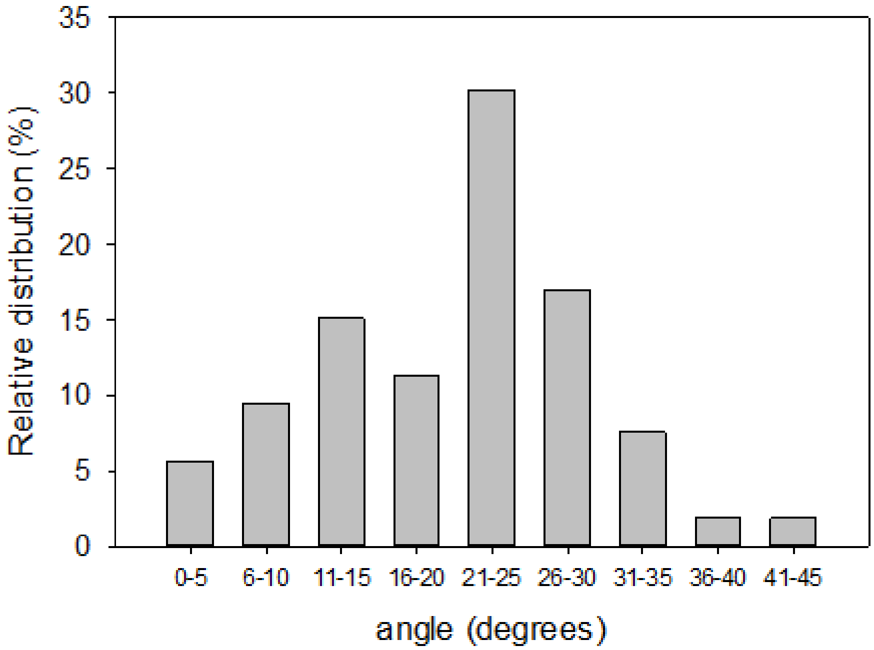

Figure 6.

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