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Advanced canopy regeneration: an unrecognized mechanism of forest dynamics

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Gaps in the forest canopy, created by tree falls, are fundamental to the process of forest dynamics (Yamamoto 2000). Tree-fall gaps are critical for the regeneration of shade-intolerant tree species while at the same time, providing opportunities for the growth and establishment of shade-tolerant tree species (Yamamoto 2000). Gap dynamics is central to understanding change in old-growth forests, and for predicting successional trends and the processes that explain the present structure and composition of tropical and temperate forest communities in the absence of large-scale disturbances (Yamamoto 2000, Muscolo et al. 2014).

The dynamics of temperate rainforests in southern Chile and westernmost Argentina is strongly dependent on the development of tree-fall gaps (Armesto et al. 1996*a*, Veblen et al. 1996). These forests share many taxa with Australian, New Zealand, and tropical South American forests because of their common Tertiary origin, and are considered a global biodiversity hotspot due to the high representation of endemic species (nearly 90% of all woody species), which in turn are threatened by high rates of deforestation and biodiversity loss (Armesto et al. 1996*b*, Miranda et al. 2017).

Since 2005, we have been exploring biodiversity in the largely unknown canopies of Chilean temperate rainforests. While doing fieldwork in the Guabún forest site, Chiloé Island (41° S), we frequently observed tree seedlings and saplings that rooted in the canopy of tall trees, even above 20 m (Fig. 1). First, we considered these observations resulted from the accidental epiphytic habit of tree seedlings (e.g., Hoeber et al. 2019); however, in a later visit to the Guabún forest in 2014, we found a large recently fallen tree (less than one year ago) covered with numerous tree seedlings and saplings up to 2 m tall. A close examination revealed that most seedlings were rooted in the thick arboreal soil held on the crown branches and the main trunk. Many of these tree seedlings and saplings were alive, with their stems growing parallel to the soil surface, but their apical buds pointing upwards towards the sunlight. We concluded that these tree seedlings and saplings were originally established in canopy branches and survived the fall of the supporting tree, constituting a regeneration cohort fully originated in the canopy. For us, this was an "*aha*" moment: young trees established on canopy before the tree fall could represent a form of advanced regeneration, that after opening of a canopy gap could gain a competitive advantage over seedlings rooted in the forest-floor or germinating from seeds. In the present work, we document for the first time the numerical importance of this "advanced canopy regeneration" (hereafter ACR) for the recovery of forest cover, diversity, and tree species composition following gap dynamics in Chilean temperate rain forests. We finally consider whether ACR could be a relevant phenomenon in other forests around the world.

From 2017 to 2019, we assessed the abundance and diversity of ACR occurring on trees and within tree-fall gaps at two privately protected forest sites: (1) Bosque

FIG. 1. Advanced canopy regeneration in Chilean temperate rainforests. (A) Seedling of *Nothofagus dombeyi* found 25 m above the ground on a dead limb of a large *N. dombeyi* tree in Bosque Pehuén Park. (B) The arrow points to a group of saplings of *Drimys winteri* growing on a large branch of a tree of *Eucryphia cordifolia* at a height of 15 m in the Guabún Forest. (C) The largest regenerating tree found in the canopy: a small individual of *N. dombeyi* 12 cm in diameter at the base and 59 yr old, growing 15 m above the ground on a large tree of *N. dombeyi*. (D) The oldest tree regenerating in the canopy: a small tree of *Nothofagus nervosa* 10 cm in diameter at the base and 114 yr old, growing 8.4 m above the ground on a large tree of *N. dombeyi*. [Color figure can be viewed at wileyonlinelibrary.com]

Pehuén, in the southern Chilean Andes (39°26′ S), and (2) Guabún forest, on the coastal lowland of Chiloé Island, southern Chile (41°47′ S). In Bosque Pehuén, we recorded the presence of ACR in all trees with diameters at the breast height (dbh) >5 cm within 24, 50-m long transects, 2-m wide, 50-m apart from one another, along a trail in the old-growth forest. We also climb six large and old trees to count and tag any ACR present, and we monitored the regeneration in two recently formed (2017 and 2018) tree-fall gaps. In Guabún forest, on the year 2019 we surveyed the regeneration present in the tree-fall gap originated in 2014. We collected cores and cross-sections of ACR to know the dates of establishment of individuals. We classified as "seedlings" all young trees less than 1 m tall and as "saplings" all trees taller than 1 m but <5 cm dbh. Woody species with a dbh > 5 cm, but <2.5 m tall were classified as "small trees." A detailed description of the study areas and sampling methods is available in the Appendix S1.

In Bosque Pehuén we sampled 99 trees along the transects, from 6.7 to 197 cm dbh. We found that 21% of the sampled trees had seedlings or saplings in their crowns. All trees with ACR had a dbh wider than 67 cm (mainly identified as *N. dombeyi* and snags) with 2.1 ± 0.2 (mean ± SE) seedlings or saplings per tree, rooted in cavities filled with woody debris and in branching points with clumps of arboreal soils. Using logistic regression analysis, we estimated that the probability that a *Nothofagus* tree had ACR increased to nearly 1 when trees were ≥ 1 m dbh (Appendix S1, Fig. S1). From this analysis we estimated the number of trees with ACR per ha, determining that between approximately 21 and 64 trees/ha had ACR in the surveyed area of Bosque Pehuén.

All trees we climbed hosted ACR, with 4.0 ± 1.6 juvenile individuals per tree with a mean age of 37 ± 15 yr old and stem diameters of 4.6 ± 1.9 cm (Appendix S1: Table S1). ACR was established between 8 and 28 m above the ground. The largest individual established in the canopy was found at a height of 15 m along the main trunk and corresponded to a small *N. dombeyi* tree (12 cm stem diameter, measured at its base), around 2.5 m tall and 59 yr old (Fig. 1). The oldest canopy individual sampled was located 8.4 m above the ground and corresponded to a small tree of *N. nervosa* (10 cm stem diameter at its base), which had few sprouts from its base, less than 1 m long; this tree was 114 yr old! (Fig. 1). Finally, within the two tree-fall gaps sampled, we identified four and six canopy-originated seedlings respectively, 75% of which were still alive and growing in 2019 (Appendix S1: Fig. S2). These seedlings represented >75% of the total number of seedlings located in these gaps.

In Guabún, in Spring 2019 we resampled the canopy gap previously found in 2014. We identified 17 saplings in the gap, 14 of them belonging to the pioneer tree species *Drymis winteri* (Winteraceae). Thirteen of the 17 saplings were clearly established before the large *E. cordifolia* tree came down. These 13 saplings had epicormic shoots growing directly from horizontal stems (Fig. 2). Sapling ages ranged between 15 and 48 yr old, meaning that they were already between 11 and 44 yr old when the tree fell (Appendix S1: Table S1). Tree-ring widths of two of these saplings showed a pronounced growth increment right after 2014 (Appendix S1: Fig. S3), which may represent a release from previous suppression.

Since 2014, we surveyed 16 forest sites between 39°S and 55°S. We detected the presence of ACR in 15 sites, usually on large old trees (Appendix S1: Table S2). Thus, tree establishment and growth in the forest canopy is a frequent phenomenon in South American temperate rainforests.

Most ACR did not show leader dieback, instead, their tree rings showed an exceptionally slow growth rate,

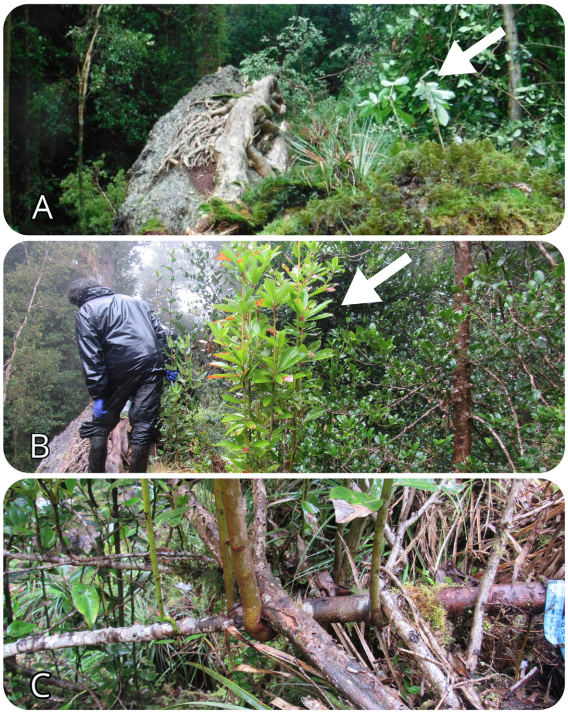

FIG. 2. Large tree-fall gap created by the massive fall of a centennial tree in 2014 in the Guabún Forest. (A) Log covered by epiphytes and canopy-originated saplings of *Drimys winteri* (Winteraceae) oriented parallel to the ground, indicated by the arrow. Photo dates back to July 2014. (B) Photo of the same log as in panel A, taken in October 2019, showing the vigorous growth and development of the same saplings. (C) View of epicormic development of new branches on a horizontal stem of the canopy sapling shown in photos A and B. This particular individual has a minimum age of 18 yr and became established in the canopy when the fallen tree was still alive. [Color figure can be viewed at wileyonlinelibrary.com]

looking more like a "bonsai" tree than a common ground-rooted seedling (Appendix S1: Fig. S4). ACR may be favored by accessing to full sunlight and lower herbivory pressure in the canopy but may suffer from restrictive supply of water or nutrients. The increase in size of ACR within the tree-fall gaps observed (Fig. 2 and Appendix S1: Fig. S2), and the strong increase in growth rates recorded after the tree fall (Appendix S1: Fig. S3) suggests that the light on the ground favors seedling and sapling development.

Several studies in Chilean temperate rainforests as well as in other forests of the world have shown the crucial importance of logs and woody debris as substrates for juvenile trees (Harmon et al. 1986, Christie and Armesto 2003). The ACR was established over branches that will become logs, covered by abundant arboreal soils and cavities with dead woody debris that can facilitate seedling persistence in the canopy. Once a tree-fall gap forms, ACR can remain attached to the fallen tree trunk accessing enhanced light and nutrients within the canopy gap. We hypothesize that ACR can have a competitive advantage over ground-rooted regeneration and may eventually dominate the area where the forest canopy gap forms.

Late-successional Chilean rainforests are characterized by the persistence of shade-intolerant pioneering trees due to the extended longevity of pioneers (Gutiérrez and Huth 2012). The ACR includes a variety of tree species with different shade-tolerances (Appendix S1: Table S2). This may favor the establishment of shade-intolerant species as well as moderately shade-tolerant, contributing to explain their persistence in old-growth forests, and the maintenance of tree diversity in the long-term.

ACR is taking place in many forest ecosystems. In old-growth forests of the Smoky Mountains (USA), Sharp (1957) described that the epiphytic habit was frequent in five species of trees, also indicating that some epiphytic individuals had over three inches in diameter and were able to reproduce. In European temperate rainforests, Hoeber et al. (2019) reported that at least 10 tree species had seedlings occurring in forest canopies, while in Canadian forests, Burns (2010) classified seedlings from two tree species as facultative epiphytes. In New Zealand, trees often regenerate on stems of tree-ferns, evidencing their ability to recruit on canopies (Gaxiola et al. 2008). Even in urban areas, Brandes (2007) reported at least four tree species occurring on top of palm trees of Croatia. In streets of the city of Valdivia, Chile (40° S), we observed juveniles of North American tree species growing epiphytically, documenting their potential to recruit and survive in the canopy for several years (Appendix S1: Fig. S5). Then, ACR seems to be relevant to forest dynamics across many forests, but still poorly understood. Although forests are three-dimensional ecosystems, most forest dynamics models provide a ground-based perspective (e.g., Shifley et al. 2017). The inclusion of the third dimension, considering ACR, remains a relevant challenge.

The old-growth forest condition has presumably prevailed for most of the history of forests (Wirth 2009). During the 20th century and before, most accessible forests have been logged, cleared, thinned, or managed, converting intact, old-growth stands into rare occurrences, which made young, even-aged, secondary forests globally widespread (Watson et al. 2018). Past and current logging practices may not resemble in any way the forms of natural disturbance under which forest evolved (e.g., Lindenmayer and McCarthy 2002). Then, the current forest remnants in managed landscapes may lack the mechanisms of tree recruitment characterizing old-growth forests. ACR could, therefore, represent a mechanism absent from managed ecosystems. Across the globe, remnant intact old-growth forests, especially in the temperate region, are few and remain largely unprotected. These ecological systems are irreplaceable and can teach us how forests really work, providing us with reference ecosystems to evaluate the effects of management techniques and restoration practices that can enhance forest recovery after disturbance (Wirth 2009, Watson et al. 2018).

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