



RESEARCH ARTICLE

Mycotrophy in Gilliesieae, a threatened and poorly known tribe of Alliaceae from central Chile

Micotrofia en Gilliesieae, una tribu amenazada y poco conocida de Alliaceae de Chile central

GUSTAVO A. TORRES-MELLADO¹, INELIA ESCOBAR¹, GÖTZ PALFNER¹ & M. ANGÉLICA CASANOVA-KATNY^{2,*}

¹Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, P.O. Box 160 C, Concepción, Chile

²Centro de Biotecnología, Universidad de Concepción, P.O. Box 160 C, Concepción, Chile

*Corresponding author: angecasanova@gmail.com

ABSTRACT

The five known genera of Gilliesieae have their diversity center in the Mediterranean zone of central Chile, where many of their habitats are threatened by urban expansion, industrial and agroforestry activities, as well as other anthropogenic impacts. Very little is known about the biology of these particular geophytes, the majority of which currently have either vulnerable or endangered status, mainly due to their dispersed and small populations generally associated to remnants of native vegetation. As mycorrhizal associations are essential for soil resource acquisition and stress mitigation in most plants, our objective was to assess the hitherto unknown mycotrophic status of ten species of Gilliesieae from central Chile by qualitative and quantitative assessment of intraradical fungal structures. All sampled genera (*Gethyum*, *Gilliesia*, *Miersia*, *Solaria*, *Speea*) showed regular presence of arbuscular mycorrhiza, while other mycorrhizal or putatively mutualistic associations, like dark septate endophytes, were practically absent. Mycorrhizal colonization of fine roots reached a mean of ca. 45 % across all examined taxa, with highly variable values ranging from 9 % to 82 % in *Miersia tenuiseta* and *Gilliesia curicana*, respectively. The high level of mycorrhization indicates that arbuscular mycorrhiza should be considered for conservation strategies of threatened species or biotechnological use in plant propagation. The main future task is the identification of the associated fungal taxa.

Key words: endangered species, Glomeromycota, latitudinal transect, Mediterranean climate, Monocotyledoneae.

RESUMEN

Los cinco géneros conocidos de Gilliesieae tienen su centro de diversidad en la zona mediterránea de Chile central, donde muchos de sus hábitats están amenazados por la expansión urbana, actividades industriales y agroforestales, así como otros impactos antropogénicos. Se sabe muy poco sobre la biología de estas particulares geófitas, que en la actualidad tienen en su mayoría estatus de vulnerable o en peligro de extinción, debido a sus poblaciones dispersas y pequeñas, generalmente asociadas a remanentes de vegetación nativa. Dado que las asociaciones micorrícicas son esenciales para la adquisición de recursos del suelo y para la mitigación de estrés en la mayoría de las plantas, nuestro objetivo fue determinar el estatus micotrófico aún desconocido de diez especies de Gilliesieae de Chile central, mediante análisis cualitativos y cuantitativos de las estructuras fúngicas intrarradicales. Todos los géneros evaluados (*Gethyum*, *Gilliesia*, *Miersia*, *Solaria*, *Speea*) mostraron la presencia regular de micorrizas arbusculares, mientras que otras asociaciones micorrícicas o asociaciones putativamente mutualistas, como los endófitos de septos oscuros, estuvieron prácticamente ausentes. La colonización micorrícica de raíces finas alcanzó un promedio de ca. 45 % en todos los taxones examinados, con valores muy variables entre 9 % a 82 % en *Miersia tenuiseta* y *Gilliesia curicana*, respectivamente. El alto nivel micorrícico encontrado indica un rol importante de la micorriza arbuscular en futuras estrategias de conservación de especies amenazadas y en su aplicación biotecnológica en la propagación de plantas. La principal tarea futura es la identificación de los taxones fúngicos asociados.

Palabras clave: clima mediterráneo, especies amenazadas, Glomeromycota, Monocotyledoneae, transecto latitudinal.

INTRODUCTION

The Gilliesieae Lindl. are a poorly known South American tribe of the Alliaceae whose most studied feature so far has been floral morphology, which mimics insects in several species (Ravenna 2000, Rudall et al. 2002). The

highest diversity of the group is encountered in central Chile, with about 14 species belonging to the five genera *Gilliesia* Lindl. (5 species), *Miersia* Lindl. (5), *Solaria* Phil. (1), *Speea* Loes. (1) and *Gethyum* Phil. (2) (Muñoz et al. 2000, Ravenna 2005, Escobar 2012) (Fig. 1). Some taxa are also known from

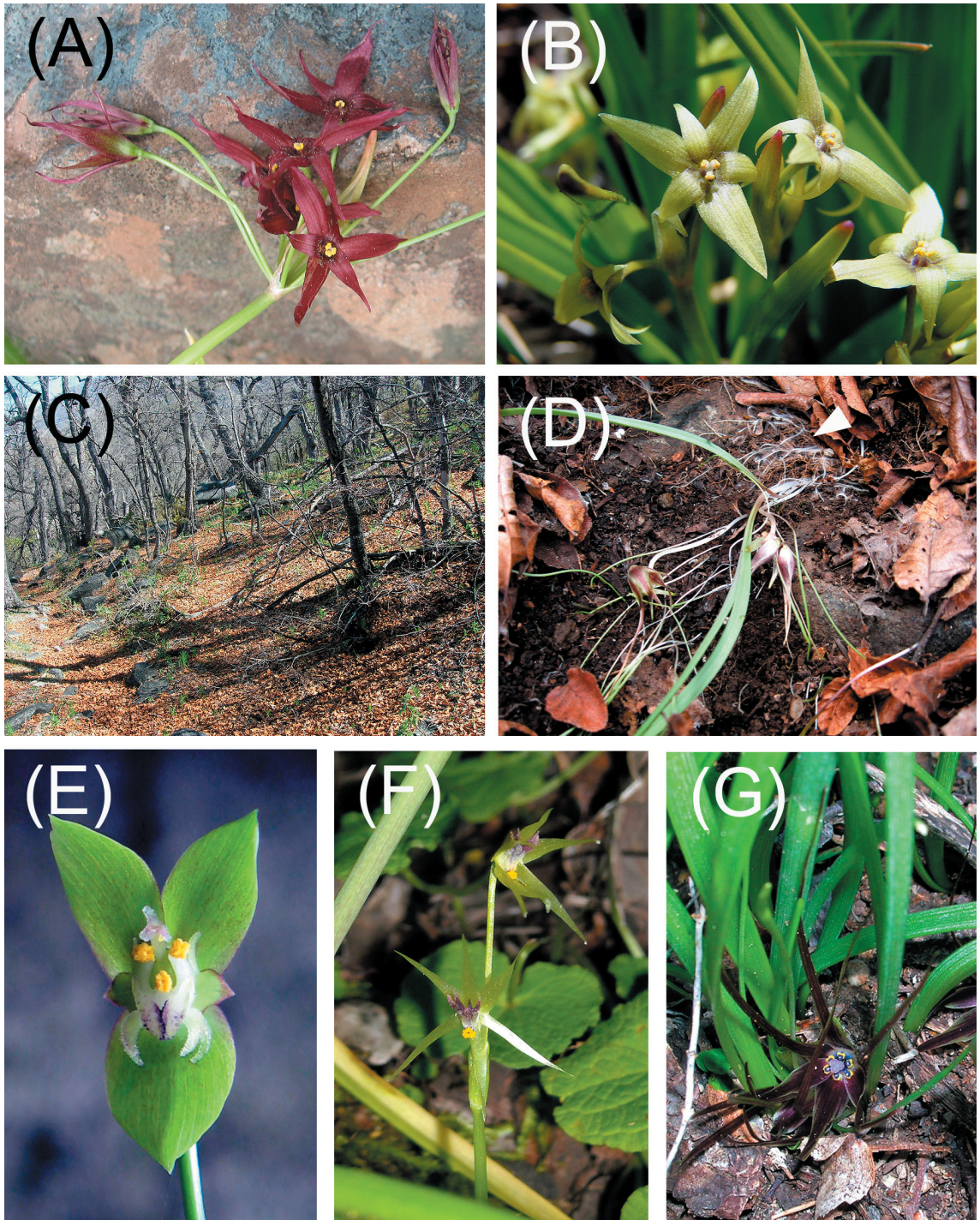


Fig. 1: Morphology of Chilean Gilliesieae in natural environment; (A) *Gethyum atropurpureum*; (B) *Solaria miersioides*; (C) early spring aspect of *Nothofagus macrocarpa* forest, with *Speea humilis* in understory; (D) *Speea humilis* with exposed fine roots under removed leaf-litter (arrowhead); (E) *Gilliesia graminea*; (F) *Miersia chilensis*; (G) *Speea humilis*; subfigures (C), (F) and (G) by Lucía Abello.

Morfología de Gilliesieae chilenas en su ambiente natural; (A) *Gethyum atropurpureum*; (B) *Solaria miersioides*; (C) aspecto del bosque de *Nothofagus macrocarpa* en la primavera temprana, con *Speea humilis* en el sotobosque; (D) *Speea humilis* con raíces finas expuestas luego de remover la hojarasca (flecha); (E) *Gilliesia graminea*; (F) *Miersia chilensis*; (G) *Speea humilis*; subfiguras (C), (F) y (G) por Lucía Abello.

Argentina, Bolivia and Peru. Most species typically grow in the Mediterranean climate zone of central Chile between 33° and 38° S, which is considered a hotspot of biodiversity (Arroyo et al. 1999). Populations are found in the understory of, or close to, native forest dominated by sclerophyllous and deciduous trees. Distribution and population size is very heterogeneous across species (Escobar et al. 2010) and the majority is classified as endangered (Ravenna et al. 1998), due to overlapping of their main distribution area with the most densely populated urban and rural zones as well as the centers of agriculture and forestry in the country. The recent, major revision of Chilean Gilliesieae by the second author (the first since Reiche 1893 and Hutchinson 1939) was based on freshly collected material of most recorded species, some of them very rare. This gave us the opportunity to scrutinize for the first time the presence of mycorrhizal associations in species of all known Chilean genera.

Generally, ecology of Gilliesieae, especially association with other organisms like soil microorganisms, pathogenic (Jackson 1926) and mutualistic fungi, pollinators, etc., to date remains largely unknown. Knowledge of mycotrophism is especially important for understanding acquisition of soil resources by Gilliesieae and their possible integration into interspecific mycorrhizal networks. In other Alliaceae and related monocot families, arbuscular mycorrhizal associations are commonly found (Wang & Qiu 2006). The arbuscular mycorrhizal (AM) symbiosis is one of the most important and widespread mutualistic associations between absorbing roots and soil fungi of the phylum Glomeromycota (Schüssler et al. 2001, Smith and Read 2008). The primary benefit of the mycorrhizal association for the plant host is the extension of its bioactive zone in the soil via fungal mycelia and mycorrhizal networks. This allows a more efficient access to soil water and nutrients (Smith & Read 2008) as well as a wider range of allelopathic protection (Sikes 2010, Barto et al. 2011), therefore having a direct effect on plant performance and community structure. The relative contribution of the mycobionts to the mentioned benefits has been shown to be species-specific (Lendenmann et al. 2011). This implies that

investigation of the general mycotrophic status of endangered plant species should be followed by an assessment of the mycorrhizal fungal species involved. Both natural mycorrhization and application of mycorrhizal fungal inocula have been shown to be efficient in restoration processes (Herrera et al. 1993, White et al. 2008). As a first step, we analyzed presence and abundance of arbuscular mycorrhizal fungal structures in roots of ten species belonging to five genera of Gilliesieae (Fig. 1), providing the first dataset about mycotrophism in this particular and interesting plant group.

METHODS

Study site

Chilean Gilliesieae were sampled from central Chile between 33°11' S (Región Metropolitana, Santiago) and 37°28' S (VIII Región, Biobío). The sampling zone is generally characterized by a temperate climate but is heterogeneous in terms of precipitation regime and temperatures along latitudinal and altitudinal gradients, which results in a mosaic of different ecosystems and habitats. The northern part of the zone is characterized by dry summers lasting seven to eight months, less than 40 mm of rain per month and almost 80 % of rainfall in winter, and low relative humidity (annual mean 70 %); also there is a high thermal amplitude with almost 13 °C difference between the warmer and colder months; daily maximum and minimum difference ranges between 14 and 16 °C (Dirección Meteorológica de Chile, <http://www.meteochile.gob.cl/>).

The southern range is characterized by a shorter summer (less than four months), precipitations up to 1300 mm per year and winter rainfall making up 65-70 % of annual total precipitation. The proximity to the ocean produces a narrower annual thermal amplitude with 7.5 °C difference between the warmer and colder months; similarly, daily thermal amplitude is only reaching up to 10 °C (Dirección Meteorológica de Chile, <http://www.meteochile.gob.cl/>)

Habitat

The collected plants were growing associated to patches of native, mostly woody vegetation, dominated by *Nothofagus* spp. (Fig. 1C) such as *N. obliqua* (Mirb.) Oerst., *N. glauca* (Phil.) Krasser, *N. dombeyi* (Mirb.) Oerst., *N. macrocarpa* (A. DC.) F.M. Vázquez & R. Rodr., *N. alexandrii* Espinosa, and sclerophyllous species like *Lithraea caustica* (Molina) Hook. & Arn., *Quillaja saponaria* Molina, *Peumus boldus* Molina or *Cryptocarya alba* (Molina) Looser. Typical habitats are roadsides, slopes, ravines or forest understory where other herbs and grasses are usually absent, at least in early spring when flowering of most Gilliesieae occurs. The selected sampling sites were recorded and categorized by habitat as: (a) Native forest: any location with predominance of native vegetation, including paths; (b) Wayside: sides of gravel or asphalt roads and highways; and (c) Plantation: forestry monocultures, including interior forest roads (Table 1).

Sampling, processing and staining of arbuscular mycorrhizal roots

Between early and mid spring (August-October) of 2007, the roots of 10 previously identified species of Gilliesieae were collected (Table 1). Notably, populations of some species were very small so that sampling had to be restricted to the minimum in order to avoid major damage. Roots were dug out, cut at the hypocotyl, cleaned with distilled water and stored in Falcon tubes in a cooler for transport. In the laboratory, the material was carefully washed in tap water to remove soil particles and debris, and then fixed in 70 % ethanol. Before staining, the roots were cleared in 10 % KOH solution at 121 °C for 20 min, subsequently washed with distilled water and stored in water/lactic acid/glycerol, according to Brundrett et al. (1996).

The staining of the AM fungal structures was performed in 10 ml Eppendorf tubes with Trypan Blue 0.01 % at 121 °C for 20 min. Before microscopy, roots were rinsed with distilled water and deposited overnight in Falcon tubes with lactoglycerol to remove excessive stain. Selected root segments were then mounted on glass slides in lactoglycerol and observed under a light microscope (Leitz Dialux, Leitz, Wetzlar, Germany) at distinct magnifications (100x to 1000x). Details of root and mycorrhizal structures were documented by digital photomicrographs using a Nikon Coolpix 950 camera (Nikon, Tokyo, Japan).

Relative mycorrhization

Percentage of mycorrhization was calculated using the Trouvelot method (Trouvelot et al. 1986, also cited in Covacevich et al. 2001). For every specimen examined, twenty 1 cm segments of stained fine roots were mounted in parallel on a slide and observed at 40x magnification. Every root segment was assigned to one of six categories (0-5) of relative mycorrhization (intensity of colonization by mycorrhizal fungal structures) ranging from 0 % to > 95 % mycorrhization. The mycorrhization percentage was then calculated as follows:

$$M_{\text{Trouvelot}} (\%) = (n_1 + 5n_2 + 30n_3 + 70n_4 + 95n_5) / N$$

N is the number of observed segments, n₁ to n₅ represent the number of segments categorized as one to five respectively. The mycorrhization percentage was obtained for each plant (Covacevich et al. 2001). When diagnostic mycorrhizal structures were observed in more than three samples (n > 3) of each species, we calculated the mycorrhization percentage and the frequency of each element (hyphal coils, intraradical hyphae, vesicles, arbuscules).

RESULTS

Roots of all examined genera showed one or more diagnostic structures of arbuscular mycorrhizae (Table 1, Fig. 2), viz.: appressoria, aseptate hyphae, hyphal coils, arbuscules, and vesicles. Differences between colonization patterns and morphology of individual structures (e.g., Fig. 2C, 2D) suggest the presence of more than one species of

arbuscular mycorrhizal fungi (AMF). Other fungus-root associations that could be expected, such as dark septate endophytes (DSE), were practically absent, with septate hyphae only found in *G. curicana*.

Mean relative mycorrhization was about 45 % across several examined species (Table 1); the highest mean value was found in *Gilliesia curicana* (82 %) and the lowest in *M. tenuiseta* (9 %, Table 1). Typical mycorrhizal structures (arbuscules, vesicles, intraradical hyphae and hyphal coils) were regularly observed, although frequency of each structure varied considerably between plant species (0-100 %, Table 1), with the most frequent elements being intraradical hyphae and vesicles (Table 1).

DISCUSSION

Arbuscular mycorrhizas are regularly present in Chilean Gilliesieae and, based on our data, seem to be the exclusive form of mycorrhizal symbiosis in this plant group. The range of relative mycorrhization found across all examined species of Gilliesieae is in concordance with available data of AM colonization of plants in natural ecosystems (Read et al. 1976, Smith & Read 2008, Treseder & Cross 2006). Morphological differences between diagnostic intraradical fungal structures such as vesicle shape, hyphal patterns and staining intensity across or within plant host species suggest the presence of more than one species of AMF, a common situation in herbaceous plants (Smith & Read 2008). Other typical fungus roots associations like DSE were practically absent, with some endophytic, dark septate hyphae found only in roots of *G. curicana*.

Differences in the phenology of diagnostic fungal structures appear across samples with some roots only showing either vesicles or arbuscules. Apart from taxon-specific traits of involved glomeromycotan fungi, this could be an expression of seasonal dynamics of mycorrhiza formation which is not backed by our data obtained from a one-off sampling campaign. Different AM structures were present in root samples from all visited habitats (plantation, native forest and wayside), without a characteristic trend. Nevertheless, the highest value of AM percentage was found in the wayside samples. It has been shown that

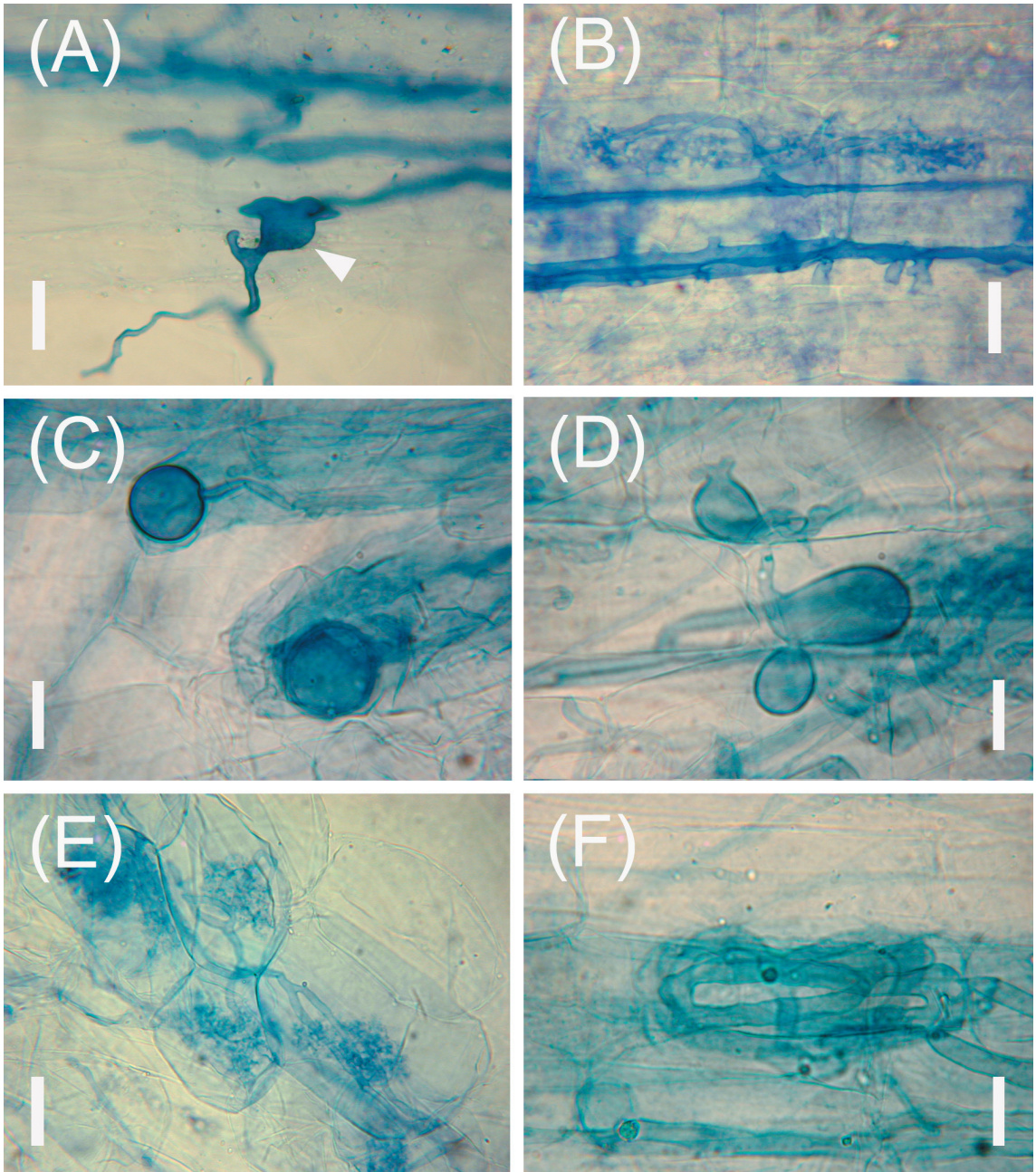


Fig. 2: Diagnostic arbuscular mycorrhizal structures in fine roots of Gilliesieae from Chile; (A) appressorium and entry point (arrowhead) on root surface of *Gilliesia graminea*; (B) extracellular runner hyphae bearing intracellular arbuscule in *Gilliesia graminea*; (C) globular vesicles in *Gilliesia curicana*; (D) irregularly shaped and ramified vesicles in *Gilliesia curicana*; (E) arbuscules in *Gilliesia graminea*; (F) hyphal coil in *Miersia chilensis*; bar for all Figs. = 20 μm (400 \times magnification).

Estructuras diagn3sticas de micorriza arbuscular en raices finas de Gilliesieae de Chile; (A) apresorio y punto de entrada (flecha) en superficie de raiz de *Gilliesia graminea*; (B) hifas corredoras extracelulares produciendo arbusculos intracelulares en *Gilliesia graminea*; (C) vesiculas globulares en *Gilliesia curicana*; (D) vesiculas de forma irregular y ramificadas en *Gilliesia curicana*; (E) arbusculos in *Gilliesia graminea*; (F) lazo hifal en *Miersia chilensis*; barra para todas las Figs. = 20 μm (400 \times aumento).

TABLE 1

Mycorrhizal percentage (M %) and frequency (%) of arbuscular mycorrhizal structures in species of Gilliesiae from central Chile. Habitats: NF = native forest, WS = wayside, PL = plantation. Arbuscular mycorrhizae structures: HC = hyphal coils, IH= intraradical hypha, Arb = arbuscules, Ves = vesicles. Mycorrhization values are means \pm SD. * n was too low for mean calculation, +: present, but frequency was not determined.

Porcentaje de Micorrización (%) y frecuencia (%) de estructuras de micorrizas arbusculares en especies de Gilliesiae de Chile central. Hábitats: NF = bosque nativo, WS = borde de camino, PL = plantación. Estructuras de micorriza arbuscular: HC = lazo hifal, IH= hifa intrarradical, Arb = arbuscúlos, Ves = vesículas. Valores de Micorrización corresponden a medias \pm DE. * n fue muy bajo para cálculo de la media, +: presente, pero su frecuencia no fue determinada.

| Species | Habitat | M % | Frequency of mycorrhizal structures | | | |
|--|------------|-------------|-------------------------------------|-----|-----|-----|
| | | | HC | IH | Arb | Ves |
| Gethyum | | | | | | |
| <i>G. atropurpureum</i> Philippi | NF | * | + | + | + | + |
| Gilliesia | | | | | | |
| <i>G. curicana</i> Ravenna | WS | 82 \pm 14 | 50 | 100 | 50 | 100 |
| <i>G. graminea</i> Lindley | WS, NF | 46 \pm 18 | 50 | 100 | 100 | 100 |
| <i>G. montana</i> Poeppig | NF, PL | 59 \pm 31 | 25 | 100 | 50 | 100 |
| Miersia | | | | | | |
| <i>M. chilensis</i> Lindley | NF, PL, WS | 52 \pm 27 | 64 | 100 | 55 | 91 |
| <i>M. leporina</i> Ravenna | NF | * | 0 | + | 0 | + |
| <i>M. minor</i> Kunth | NF | * | + | + | 0 | + |
| <i>M. tenuiseta</i> Ravenna | NF | 9 \pm 14 | 40 | 100 | 20 | 100 |
| Solaria | | | | | | |
| <i>S. miersioides</i> Philippi | NF | 27 \pm 19 | 0 | 100 | 0 | 100 |
| Speea | | | | | | |
| <i>S. humilis</i> (Phil.) Loes. ex K. Krause | NF | * | 0 | + | 0 | 0 |

soil disturbance by human activities can lead to changes in AMF communities, especially by reducing their diversity, given that different genera respond differently to such disturbance (Dodd 2000). This has been extensively proven in agricultural soils where AMF species vanish over longer periods of regular tillage (e.g., Jansa et al. 2002, Oehl et al. 2005). Jha et al. (1992) found that in degraded forest habitats, AMF populations were smaller than in less disturbed sites.

Quality and quantity of mycorrhization in Chilean Gilliesiae is probably relevant for its conservation status as well: many of their habitats which are mostly located in the Mediterranean zone of central Chile, are patchy, having suffered from land use changes, especially during the last decades, and are degraded or surrounded by agricultural land or exotic forestry plantations (Arroyo et al. 1999). It has been shown that the

stability and diversity of plant communities and soil microbial communities (including AMF) are mutually correlated and that common mycorrhizal networks can structurally and functionally connect not only roots of conspecific host individuals but also of different plant species in a defined area (Haystead et al. 1988; McNaughton & Oosterheld 1990, van der Heijden & Horton 2009). Whereas Gilliesiae grow preferentially on spots where other herbaceous plants are, at least seasonally, rare or absent, they are often found close to native tree species like *Cryptocarya alba* (Lauraceae), *Quillaja saponaria* (Rosaceae) and *Peumus boldus* (Monimiaceae), among others (personal observation), which have been shown to form AM as well (Garrido 1988, Godoy et al. 1991, Carrillo et al. 1992). This could be a hint for the existence of shared mycorrhizal mycelia which so far in Chilean monocots has only been shown for the achlorophyllous and obligate

mycoheterotrophic *Arachnitis uniflora* Phil. (Corsiaceae) (Carrillo et al. 1992, Bidartondo et al. 2002). Under this scenario, the progressive loss of native vegetation and secondary effects like erosion and other types of soil disturbance or contamination could reduce diversity of the AMF community (Abbott & Robson 1991, Jha et al. 1992, Helgason et al. 1998, Dodd 2000) and, consequently, potential mycobionts for Gilliesieae. On the other hand, treatment of endangered plant species and/or degraded habitats with inoculum of adequate mycorrhizal fungi has been shown to yield positive effects on regeneration (Herrera et al. 1993, Moora et al. 2004, Vergeer et al. 2006, White et al. 2008).

In this context, future work should be focused on the dependency of Gilliesieae on common mycorrhizal networks and the identification of the associated fungal species. Apart from the potential significance of mycorrhiza for restoration practices (Haselwandter 1997), it has been shown that despite of the worldwide distribution of many AMF taxa, there seems to be a more specific relationship between certain, possibly locally adapted species and their plant hosts (van der Heijden 1998, Klironomos 2003, Vogelsang et al. 2006).

ACKNOWLEDGEMENTS: We would like to thank Lucía Abello who kindly provided the high quality pictures of some species of Gilliesieae in Fig. 1. We also appreciate the comments of two anonymous reviewers and the associated editor which allowed important improvements of the original manuscript. G.A. Torres-Mellado would like to thank the Chilean National Council for Science and Technology CONICYT for the assigned Postgraduate Grant.

LITERATURE CITED

- ABBOTT LK & AD ROBSON (1991) Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. *Agriculture, Ecosystems & Environment* 35: 121-150.
- ARROYO MTK, JR ROZZI, J SIMONETTI, PA MARQUET & M SALABERRY (1999) Central Chile. In: Mittermeier RA, N Myers, P Robles-Gil & CG Mittermeier (eds) *Hotspots. Earth's biologically richest and most endangered terrestrial ecoregions*: 161-171. Cemex-Agrupación Sierra Madre, DF, Mexico.
- BARTO EK, M HILKER, F MÜLLER, BK MOHNEY, JD WEIDENHAMER & M RILLIG (2011) The fungal fast lane: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *Plos One* 6: e27195.
- BIDARTONDO MI, D REDECKER, I HIJRL, A WIEMKEN, TD BRUNS et al. (2002) Epiparasitic plants specialized on arbuscular mycorrhizal fungi. *Nature* 419: 389-392.
- BRUNDRETT M, N BOUGHER, B DELL, T GROVE & N MALAJCZUK (1996) Working with mycorrhizas in forestry and agriculture. ACIAR Monograph 32. Australian Centre for International Agricultural Research, Canberra.
- CARRILLO R, R GODOY & H PEREDO (1992) Simbiosis micorrízica en comunidades boscosas del valle central en el sur de Chile. *Bosque* 13: 57-67.
- COVACEVICH F, HE ECHEVERRÍA, & LAN AGUIRREZABAL (2001) Comparación de dos técnicas de cuantificación de infección micorrízica. *Ciencia del Suelo (Argentina)* 19: 155-158.
- DODD JC (2000) The role of arbuscular mycorrhizal fungi in agro- and natural ecosystems. *Outlook on Agriculture* 29: 63-70.
- ESCOBAR I, P NOVOA, E RUIZ, M NEGRITTO & C BAEZA (2010) Nuevo hallazgo de *Miersia cornuta* Phil. (Gilliesieae-Alliaceae). *Gayana Botánica* 67: 130-134.
- ESCOBAR I (2012) Sistemática de la tribu Gilliesieae Lindl. (Alliaceae), sobre la base de evidencias morfoanatómicas, citológicas y moleculares. Tesis Doctoral, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile.
- GARRIDO N (1988) Agaricales s.l. und ihre Mykorrhizen in den *Nothofagus*-Wäldern Mittelchiles. *Bibliotheca Mycologica* 120. J Cramer, Berlin-Stuttgart.
- GODOY R, C RIQUELME, H PEREDO & R CARRILLO (1991) Compatibilidad y eficiencia de hongos micorrízicos vesículo-arbusculares en *Eucalyptus camaldulensis* y *Quillaja saponaria*. *Ciencia e Investigación Forestal (Chile)* 5: 237-250.
- HASELWANDTER K (1997) Soil micro-organisms, mycorrhiza, and restoration ecology. In: Urbanska KM, NR Webb & PJ Edwards (eds) *Restoration ecology and sustainable development*: 65-80. Cambridge University Press, Cambridge.
- HAYSTEAD A, N MALAJCZUK & TS GROVE (1988) Underground transfer of nitrogen between pasture plants infected with VA mycorrhizal fungi. *New Phytologist* 108: 417-423.
- HELGASON T, TJ DANIELL, R HUSBAND, AH FITTER & JPW YOUNG (1998) Ploughing up the wood-wide web? *Nature* 394: 431.
- HERRERA MA, CP SALAMANCA & JM BAREA (1993) Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified Mediterranean ecosystems. *Applied and Environmental Microbiology* 59: 129-133.
- HUTCHINSON J (1939) The tribe *Gilliesieae* of *Amaryllidaceae*. *Herbertia (USA)* 6: 136-145.
- JACKSON HS (1926) The rusts of South America based on the Holway collections: I. *Mycologia* 18: 139-162.
- JANSA J, A MOZAFAR, T ANKEN, R RUH, IR SANDERS & E FROSSARD (2002) Diversity and structure of AMF communities as affected by tillage in a temperate soil. *Mycorrhiza* 12: 225-234.
- JHA DK, GD SHARMA & RR MISHRA (1992) Ecology of soil microflora and mycorrhizal symbionts in degraded forests at two altitudes. *Biology and Fertility of Soils* 12: 272-278.
- KLIRONOMOS JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84: 2292-2301.

- LENDENMANN M, C THONAR, RL BARNARD, Y SALMON, RA WERNER, E FROSSARD & J JANSÁ (2011) Symbiont identity matters: Carbon and phosphorus fluxes between *Medicago truncatula* and different arbuscular mycorrhizal fungi. *Mycorrhiza* 21: 689-702.
- MCNAUGHTON SJ & M OESTERHELD (1990) Extramatrical mycorrhizal abundance and grass nutrition in a tropical grazing ecosystem, the Serengeti National Park, Tanzania. *Oikos* 59: 92-96.
- MOORA M, M ÖPIK, R SEN & M ZOBEL (2004) Native arbuscular mycorrhizal fungal communities differentially influence the seedling performance of rare and common *Pulsatilla* species. *Functional Ecology* 18: 554-562.
- MUÑOZ M (2000) Consideraciones sobre los géneros endémicos de monocotiledóneas de Chile. *Noticiario Mensual del Museo Nacional de Historia Natural de Chile (Chile)* 343: 16-27.
- OEHL F, E SIEVERDING, K INEICHEN, E-A RIS, T BOLLER & A WIEMKEN (2005) Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. *New Phytologist* 165: 273-283.
- RAVENNA P (2000) The family Gilliesiaceae. *Onira (Argentina)* 4: 11-14.
- RAVENNA P (2005) Especies nuevas de *Gilliesia* y *Solaria* (Gilliesiaceae) y claves para el reconocimiento de las especies de ambos géneros. *Chloris Chilensis* 8 (on line). URL: <http://www.chlorischile.cl> (accessed June 01, 2005)
- RAVENNA P, S TEILLIER, J MACAYA, R RODRÍGUEZ & O ZÖLLNER (1998) Categorías de conservación de las plantas bulbosas nativas de Chile. *Boletín del Museo Nacional de Historia Natural (Chile)* 47: 47-68.
- READ DJ, HK KOUICHEKI & J HODSON (1976) Vesicular-arbuscular mycorrhiza in natural vegetation systems. The occurrence of infection. *New Phytologist* 77: 641-653.
- REICHE K (1893) Beiträge zur Kenntnis der Liliaceae-Gilliesiaceae. *Botanische Jahrbücher für Systematik (Germany)* 16: 262-277.
- RUDALL PJ, RM BATEMAN, MF FAY & A EASTMAN (2002) Floral anatomy and systematics of Alliaceae with particular reference to *Gilliesia*, a presumed insect mimic with strongly zygomorphic flowers. *American Journal of Botany* 89: 1867-1883.
- SCHÜSSLER A, D SCHWARZOTT & C WALKER (2001) A new fungal phylum, the Glomeromycota: Phylogeny and evolution. *Mycological Research* 105: 1413-1421.
- SIKES BA (2010) When do arbuscular mycorrhizal fungi protect plant roots from pathogens? *Plant Signaling & Behavior* 5: 763-765.
- SMITH SE & DJ READ (2008) *Mycorrhizal symbiosis*. Academic Press, Cambridge.
- TRESEDER KK & A CROSS (2006) Global distributions of arbuscular mycorrhizal fungi. *Ecosystems* 9: 305-316.
- TROUVELOT A, JL KOUGH & V GIANINAZZI-PEARSON (1986) Mesure du taux de mycorrhization VA d'un système racinaire. Recherche de méthodes d'estimation ayant une signification fonctionnelle. In: Gianinazzi-Pearson V & S Gianinazzi (eds) *Physiological and genetical aspects of mycorrhizae*: 217-221. INRA, Paris.
- VAN DER HEIJDEN MGA & TR HORTON (2009) Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* 97: 1139-1150.
- VAN DER HEIJDEN MGA, T BOLLER, A WIEMKEN & IR SANDERS (1998) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79: 2082-2091.
- VERGEER P, LJJ VAN DEN BERG, J BAAR, NJ OUBORG & JGM ROELOFS (2006) The effect of turf cutting on plant and arbuscular mycorrhizal spore recolonization: Implications for heathland restoration. *Biological Conservation* 129: 226-235.
- VOGELSANG KM, HL REYNOLDS & JD BEVER (2006) Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. *New Phytologist* 172: 554-462.
- WANG B & YL QIU (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16: 299-363.
- WHITE JA, J TALLAKSEN & I CHAVAT (2008) The effects of arbuscular mycorrhizal fungal inoculation at a roadside prairie restoration site. *Mycologia* 100: 6-11.

Editorial responsibility: Ernesto Gianoli

Received August 12, 2011; accepted March 30, 2012