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Funneliglomus, gen. nov., and *Funneliglomus sanmartinensis*, a new arbuscular mycorrhizal fungus from the Amazonia region in Peru

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A new arbuscular mycorrhizal fungus was found in agricultural field sites in the Amazonia lowlands of the Department San Martin, Perú. It was found up to 858 m above sea level in two plantations of the inka nut (also called ‚sacha inchi', *Plukenetia volubilis*), which was grown in mixed cultures together with *Musa* sp., *Zea mays*, *Phaseolus vulgaris* and *Carica papaya*. The fungus was propagated in bait cultures in a greenhouse on *Sorghum* sp., *Brachiaria* sp., *Medicago sativa* and *Plukenetia volubilis* as host plants. The fungus differentiates orange brown to dark orange brown, triple-layered spores, 93–151× 90–148 µm in diameter, terminally on funnel-shaped to rarely cylindrical or slightly inflating hyphae, and a strong, straight to slightly recurved septum that closes the spore pore at the spore base. Phylogenetically, the new fungus represents clearly a new genus in a separated clade, near to *Funneliformis* and *Septoglomus*. It can easily be distinguished from all other species of these genera by the characteristic ornamentation of the spore surface, which consists of multiple large, irregular pits. The fungus is here described under the epithet *Funneliglomus sanmartinensis*, serving as type species of the new genus *Funneliglomus*.

Keywords: agroforestry, farming systems, Peruvian, Glomeraceae, Glomerales, Glomeromycetes, mountain peanut.

Taxonomy and classification of arbuscular mycorrhizal fungi (AMF; Glomeromycota) has thoroughly changed in the last two decades, basically due to concomitant advances in morphological and molecular phylogenetic identification, and by intensified soil and identification surveys in natural, agricultural and agroforestry ecosystems (e.g. Marinho et al. 2014, 2018). For instance, the gigasporoid species were re-organized in several families and genera due to their phylogeny and differences in spore wall structure, and especially in germination shield pigmentation and germ lobe or germ compartment structures (e.g. Oehl et al. 2008, Silva et al. 2012, Pontes et al. 2013). Acaulosporoid and entrophosporoid spores were also re-organized recently due to new phylogenetic findings and recognized differences in spore formation and spore morphology (e.g. Sieverding & Oehl 2006, Spain et al. 2006, Palenzuela et al. 2008, Oehl et al. 2011b, Willis et al. 2016, Lin et al. 2019). Finally, also glomoid species, by far the largest species groups within Glomeromycota, were attributed to distinct phylogenetic clades, for which characteristic spore wall structures, and especially typical pigmentation, wall structure, shape and pore closure type of the subtending hyphae at the spore base could be defined (e.g. Oehl & Sieverding 2004, Schüßler & Walker 2010, Oehl et al. 2011a, Mello et al. 2013, Sieverding et al. 2014, Błaszkowski et al. 2015).

In 2011, a new genus, *Septoglomus* Sieverd. et al., was described as a sister group of *Funneliformis* within the Glomeraceae based on concomitant mor-

phological and molecular phylogenetic spore analyses (Oehl et al. 2011a). Both genera have glomoid species with strong-conspicuous, persistent, pigmented subtending hyphae, and conspicuous septa, which generally close prominently the pore of the subtending hyphae either at the spore base or at some distance to this base (Schüßler & Walker 2010, Oehl et al. 2011a, 2019).

There are only a few studies, focusing on the diversity of AM fungi in the Amazonia lowlands in Perú (Ruíz et al. 2011, Rojas-Mega et al. 2014). In the frame of AMF diversity studies in the Amazonia lowlands and adjacent Andean low mountain ranges in the Department San Martín, we found a new species, which resembled both these genera mentioned above, due to its pronounced, generally funnel-shaped, to rarely cylindrical to constricted subtending hyphae, which usually remain persistent on soil-borne spores and generally differentiate strong septa formed at the spore base. The new fungal species was found in two plantations of the inka nut (also called 'inka peanut' or 'sacha inchi', *Plukenetia volubilis* L.). The inka nut (family Euphorbiaceae) is a perennial climbing plant, usually about 2-3 meters high, and native to the Peruvian Amazon. This plant has recently gained increasing attention also in other parts of the tropical world (e.g. Srichamnong et al. 2018, Wang et al. 2018), as its seeds can be pressed for oil production or roasted and serve as a snack, while the dried leaves can be used to make a kind of tea (Srichamnong et al. 2018). 'Sacha inchi' is also known as a novel source of oil, rich in unsaturated fatty acids (Wang et al. 2018). The objective of the present study was to describe the new fungus, associated to *Plukenetia volubilis* roots in Peru, based on both, morphological and phylogenetic analyses.

Material and methods

Study sites, soil sampling

Soil samples (0–30 cm depth) were repeatedly taken in agricultural field sites with *Plukenetia volubilis* (= inka nut, sacha inchi, or moutain peanut) of Paucarpata (06°26′26.44″S; 076°31′39.11″W; 858 m a.s.l.) and Palmiche (06°20′02.40″S, 076°36′00.00″W; 462 m a.s.l.) in Peruvian Amazonia lowlands and adjacent Andean low mountain ranges of the province Lamas in the Department San Martín. These sites were traditional agroforestry sites, where the inka nut is grown in a mixed culture with maize, beans, and other field crops without addition of chemical fertilizers and pesticides. Mean annual temperatures are about 25–27 °C, with variation between 18 and 32 °C throughout the year. Mean annual precipitation is approximately 1300 mm.

AM fungal bait cultures

Bait cultures were established in the greenhouse under ambient temperature conditions, in cylindrical 3l pots with 3 kg of substrate. The substrate consisted of a 1:1 mixture of collected field soil samples and coarse river sand. The substrate mixtures were autoclaved at 121°C for 60 min, three weeks before establishment of the bait cultures. At inoculation and bait culture establishment, the pots were first filled to 75 % with the autoclaved substrate. Thereafter 100 g of rhizospheric soils were added to the substrate surface and five seeds either of *Sorghum vulgaris* L., alfalfa (*Medicago sativa* L.), *Brachiaria* spp. and inka nut (*Plukenetia volubilis* L.) were seeded in order to establish the mycorrhizal association and reproduce spores of the new fungal species together within the complete native AMF communities. The seeds were surface sterilized before seeding, using sodium hypochlorite (0.5 %). Finally, the seeds were covered with the remaining 25% of the autoclaved substrate. The cultures were maintained in the greenhouse of the Facultad de Ciencias Agrarias, Universidad Nacional de San Martín-Tarapoto for eight months, with 21.4 °C, 29 °C and 38.2 °C as minimum, mean and maximum temperatures, respectively. The relative humidity was from 48 to 74 % between April and November 2018. The pots were irrigated every other day and fertilized with a Long Anston nutrient solution (Hewitt 1966) every two weeks, with reduced P contents (60 % reduction).

Morphological analyses

Spores of the new fungus were separated from the field soil and bait culture samples by a wet sieving process as described by Sieverding (1991). The described morphological spore characteristics and their subcellular structures are based on observations of specimens mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG; Koske & Tessier 1983), Melzer's reagent, a mixture of PVLG and Melzer's reagent (Brundrett et al. 1994), a mixture of lactic acid to water at 1:1, and in water (Spain 1990). The terminology of the spore structure basically is that presented in Błaszkowski (2012) and Oehl et al. (2015) for species with glomoid spore formation. Photographs were taken with a digital camera (Leika DFC 295) on a compound microscope (Leitz Laborlux S), using Leica Application Suite Version

V 4.1 software. Specimens mounted in PVLG and a (1:1) mixture of PVLG and Melzer's reagent were deposited at Z+ZT (ETH Zurich, Switzerland).

Molecular analyses

Intact, healthy spores were isolated from field soil and bait culture samples, and cleaned by friction on fine filter paper. Spores were surface-sterilized (Mosse 1962) using a solution of chloramine T (2 %), streptomycin (0.02 %) and Tween 20 (2–5 drops in 25 ml final volume), for 20 min and rinsed five times in milli-Q water. Intact sterilized single spores were selected under a laminar flow hood and individually transferred into Eppendorf PCR tubes. Crude extract was obtained by crushing four individual spores with a sterile disposable micropestle in 23 µL milli-Q water, as described by Palenzuela et al. (2013). Direct PCR of these crude extracts was performed in an automated thermal cycler (Eppendorf Mastercycler nexus, Germany) with a pureTaq Ready-To-Go PCR Bead (Amersham Biosciences Europe GmbH, Germany) following manufacturer's instructions with 0.4 µM concentration of each primer. A two-step PCR was conducted to amplify the ribosomal fragment consisting of partial SSU, ITS1, 5.8S, ITS2 and partial LSU rDNA using the primers SSUmAf/LSUmAr and SSUmCf/LSUmBr, consecutively, according to Krüger et al. (2009). PCR products from the second round of amplifications (~1500 bp) were separated electrophoretically on 1.2 % agarose gels, stained with Diamond™ Nucleic Acid Dye (Promega) and viewed by UV illumination. The band of the expected size was excised with a scalpel and isolated from the gel with the GFX™ PCR DNA and Gel Band Purification Kit (Sigma-Aldrich) following the manufacturer's protocol, cloned into the pCR2.1 vector (Invitrogen, Carlsbad, CA, USA) and transformed into One Shot® TOP10 chemically competent *Escherichia coli* (Invitrogen, Carlsbad, CA, USA). Recombinant colonies (15) were selected by blue/white screening and the presence of inserts detected by PCR amplification with KOD DNA Polymerase (Sigma-Aldrich) using universal forward and reverse M13 vector primers. After isolation from transformed cells, plasmids were sequenced on both strands with M13F/M13R primers using the BigDye Terminator kit 3.1v (Applied Biosystems). The products were analyzed on an automated DNA sequencer (3730xl DNA analyzer).

Phylogenetic analyses

The AM fungal sequences (partial SSU, ITS region, and partial LSU rDNA) obtained were aligned with other related glomeromycotan sequences from GenBank in ClustalX (Larkin et al. 2007). *Claroideoglomus etunicatum* (W.N. Becker & Gerd.) C. Walker & A. Schüssler was included as outgroup. Prior to phylogenetic analysis, the model of nucleotide substitution was estimated using Topali 2.5 (Milne et al. 2004). Bayesian (two runs over 5×10^6 generations, with a sample frequency of 500 and a burnin value of 25 %) and maximum likelihood (1000 bootstrap) analyses were performed, respectively, in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) and PhyML (Guindon & Gascuel 2003), launched from Topali 2.5, using the GTR + G model.

Results

Molecular analyses

The phylogenetic analyses from the partial SSU, ITS region, and partial LSU rDNA sequences placed the new fungus in a distinct clade near to *Funneliformis* and *Septoglomus* (Fig. 1). The support values for the clade of the new genus were 100 % in all analyses. In the BLASTn analysis, the rDNA sequences with closest match (87 %) to the new fungus are from *Septoglomus* and *Funneliformis* species.

Taxonomy

Funneliglomus **Corazon-Guivin, G.A. Silva & Oehl, gen. nov.**
MycoBank no. MB 829266

Diagnosis. – Spores with slightly funnel-shaped to rarely cylindrical subtending hyphae, which are concolorous with the spore and regularly have a broad, straight to slightly curved septum at the spore base.

Etymology. – *Funneli-* and *-glomus*, combining the names of the two Glomeromycetes genera *Funneliformis* and *Septoglomus* most closely related to the new genus.

Typus generis. – *Funneliglomus sanmartinensis* Corazon-Guivin, G.A. Silva & Oehl

Description. – *Funneliglomus* species differentiate spores terminally on funnel-shaped to rarely cylindrical to slightly inflating subtending hyphae, which are concolorous with the color of the spores and have a strong, straight or rarely curved, sometimes plug-like septum closing the pore at the spore base. So far, they can be clearly differentiated from *Funneliformis* and *Septoglomus* spp., besides small differences at the spore base and the subtending hyphae, by the presence of an irregular-pitted

Fig 1. Phylogenetic tree of the Glomeraceae obtained by analysis from partial SSU, ITS region, and LSU rDNA sequences of different Glomeraceae spp. Sequences are labeled with their database accession numbers. Support values (from top) are from Bayesian inference (BI) and maximum likelihood (ML), respectively. Sequences obtained in this study are in boldface. Only support values of at least 65 % are shown. Thick branches represent clades with more than 90 % of support in all analyses. The tree was rooted by *Claroideoglomus etunicatum*.

spore ornamentation, and by molecular phylogeny on the partial SSU, ITS region, and partial LSU rDNA.

***Funneliglomus sanmartinensis* Corazon-Guivin, G.A. Silva & Oehl, sp. nov.** – Figs. 2–11
MycoBank MB 829267

Diagnosis. – Differing from *Funnelformis multiforus* by orange brown spore color and smaller size, by larger size and more irregular shape of the pit ornamentations on the spore surface, and by less pronounced funnel-shaped subtending hyphae.

Etymology. – *Sanmartinensis*, referring to the State/Department San Martín in Peru, in which this species was found for the first time.

Types. – Deposited at Z+ZT (holotype ZT Myc 59767), derived from a bait culture established on the host plant inka nut (*Plukenetia volubilis*) in the greenhouse of the Molecular Biology and Genetics Laboratory, Faculty of Agricultural Sciences, National University of San Martin-Tarapoto, Peru. Fungal inoculum for the culture originated from an inka nut plantation in Palmiche (6° 20′ 2.40″ S, 76° 36′ 0″ W; 462 m a.s.l.) where the trees were cultured in agroforestry systems together with *Zea mays* and *Phaseolus vulgaris*. *Leg*. Mike Anderson Corazon Guivin on 25.03.2016. Isotypes (ZT Myc 59768) and paratypes (ZT Myc 59769) from other cultures grown on *Sorghum* and *Brachiaria* sp., and from other collection dates (15.03.2018) or other sites (Paucarpata; 06° 26′ 26.44″ S; 76° 31′ 39.11″ W; 858 m a.s.l.), in the Peruvian Amazonian lowlands were also deposited at Z+ZT. Living cultures of the fungus are currently maintained at the Universidad Nacional de San Martin-Tarapoto.

Description. – Orange brown to dark orange brown, triple-layered spores, 93–151× 90–148 µm in diam., terminally on funnel-shaped to rarely cylindrical or slightly inflating hyphae, and straight to rarely curved, often plug-like septa closing the spore pore at the spore base.

Spore wall (SW) triple-layered. Outer layer SWL1 hyaline to subhyaline, evanescent, 1.2–1.8 µm thick. SWL2 a subhyaline, evanescent to semi-persistent middle layer, and 1.5–2.8 µm thick. SWL3 orange brown to dark orange brown, persistent and finely laminate, 3.8–8.5 µm thick, and crowded with circular to ovoid, to oblong or boomerang-like, concave pits, 4.0–15.0(22) × 3.8–14.0(18) µm in diam., and 0.8–2.5 µm deep. None of the three layers staining when exposed to Melzer's reagent.

Subtending hyphae (SH) of spores straight or recurved, to rarely flared, generally funnel-shaped, to rarely cylindrical or constricted, or slightly inflating in about 10–25 µm distance from the spore base. SH 12–23 µm broad at spore base, usually tapering to 9–14 µm within 10–40 µm distance to the spore base. All three spore wall layers continuing in the subtending hyphae. SWL1 & SWL2 usually evanescent and regularly missing already on young spores. SWL3 tapering from 4.0–8.0 µm at the spore base to 1.5–3.8 µm within 10–40 µm distance from the base. Pore approximately 4.0–8.0 µm at spore base, generally closed by a strong, straight to rarely curved septum, about (1.5)2.5–5.0 µm thick.

Mycorrhiza formation. – Forming AM symbiosis with *Sorghum* sp., *Brachiaria* sp. and *Plukenetia volubilis* as plant hosts in pot cultures.

Distribution. – So far, the fungus was found in two agroforestry sites (inka nut plantations of Paucarpata and Palmiche) in the Province of Lamas, Department of San Martín, (Amazonia lowlands and adjacent low mountain ranges up to 858 m a.s.l.). Soil pH at the sites was 7.6-7.7, and available P was rather low (8–12 mg P kg^{-1}).

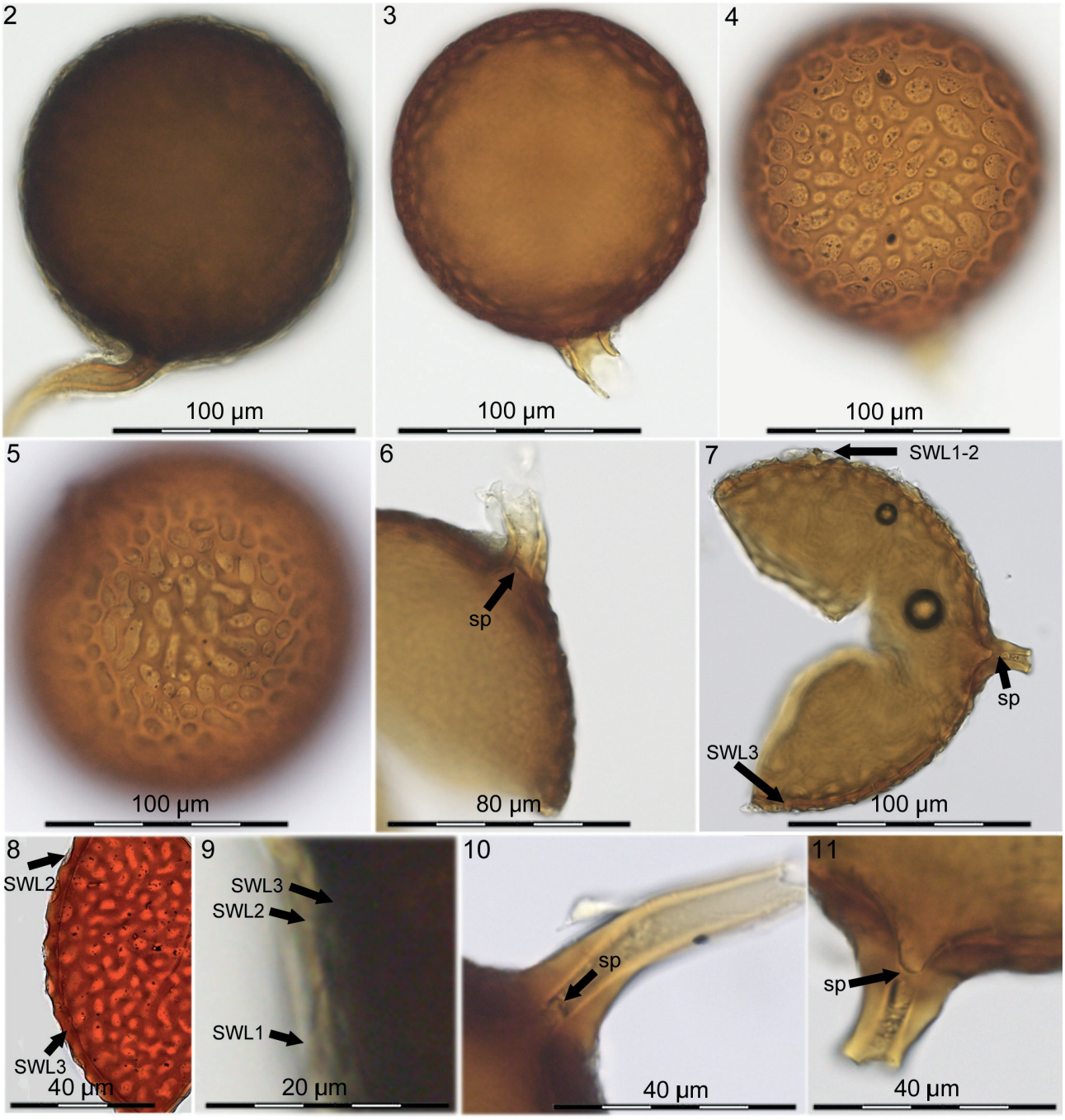
Discussion

Funneliglomus sanmartinensis can easily be distinguished from all other species in the Glomeraceae by the combination of spore color, size, and the structure of the spore and subtending hyphae, and especially by the size and shape of the pit ornamentation at spore surface. The morphologically most similar species is *Funneliformis multiforus*, which has dark yellow to brown and larger (150–220 × 180–310 µm) spores, more pronounced funnel-shaped subtending hyphae, a curved septum, and more regular and more evenly distributed pit ornamentation consisting of regular-rounded and substantially smaller pits (2.7–2.9 × 3.7–4.9 µm in diam) than *F. sanmartinensis* (Błaszkowski & Tadych 1997, Oehl et al. 2011a). So far, there is not any other of the approximately 20–25 species attributed to *Funneliformis*, *Septoglomus* or *Funneliglomus* with pitted spore surfaces.

Morphologically, the new genus *Funneliglomus* is not easily distinguished from *Funneliformis* and *Septoglomus*. However, *Funneliformis* species regularly have more pronounced funnel-shaped subtending hyphae than *F. sanmartinensis*, while *Septoglomus* species have predominantly constricted to cylindrical subtending hyphae (Oehl et al. 2019), which was rarely observed on *F. sanmartinensis* spores. Phylogenetically, *F. sanmartinensis* clearly is a new genus in a separate clade near *Funneliformis*

and *Septoglomus*. Sequences of the morphologically most closely related species *Funneliformis multiforus* are unfortunately not available for the LSU of the ribosomal gene, but available short ITS sequences prove that the later species belongs to the genus *Funneliformis* (Krüger et al. 2012).

Funneliformis and *Septoglomus* species have a worldwide distribution, from cold up to semi-arid



Figs. 2–11. *Funneliglomus sanmartinensis*. **2–7.** Orange brown to dark orange brown spores formed on generally funnel-shaped subtending hyphae. Spores triple layered (SWL1-3) with pitted surface ornamentation on SWL3. Pits easily visible in planar view due to their variable, but generally large sizes. In cross view, pits are not easily illustrated as usually rather shallow (rarely > 2.0 µm deep). **8–9.** Spore wall consisting of three layers. Here: SWL1 and SWL2 in degradation stages; SWL3 orange brown to dark (reddish) brown, making the shallow pits almost invisible in darker spores. **10–11.** Characteristic funnel-shaped subtending hyphae; spore pores at the base closed by a slightly curved to generally straight bridging septum.

subtropical and semi-humid to humid tropical climates (e.g. Błaszkowski et al. 2013, 2014, Symanczik et al. 2014, Marinho et al. 2019). So far, only 10–15 AMF species are known in each of these latter genera. It is unknown, whether *Funneliglomus* species have similar high species numbers, or can be found as frequently in different ecosystems as *Funneliformis* and *Septoglomus*. Future investigations will tell us more about the biogeography of the new genus. So far, *Funneliglomus* is considered to be restricted to the Amazonian lowlands and adjacent low mountain ranges of Peru, subjected to tropical, semi-humid to humid agroforestry systems.

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