Terrestrial litter trappers in the Golfo Dulce region: diversity, architecture and ecology of a poorly known group of plant specialists

Plantas captadoras de hojarasca en la región de Golfo Dulce: diversidad, arquitectura y ecología de un grupo de plantas especialistas poco conocido

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Abstract: Collection of forest litter and exploitation of the rotting material is a well known life strategy of epiphytic ferns and tank bromeliads. Recently, this strategy has also been discovered in terrestrial vascular plants, the so-called terrestrial litter trappers (TLTs). In the Golfo Dulce rainforests, TLTs are found in surprisingly high numbers, both in terms of species and (in places) abundance, and obviously play a significant ecological role. In the present paper, a species list with a preliminary classification of the architectural models is given and the various morphological adaptations to litter capture are described. The litter is guided either to the centre of the crown or to the base of the stem where it accumulates and decomposes. In some species, adventitious roots grow into the decaying litter to take up nutrients; in others, the plants profit from the nutrient-rich stem flow, thus gaining advantage over normal, ground-rooting plants. Litter trapping obviously represents a short cut of the litter fall cycle and therefore an adaption to nutrient-poor rainforest soils.

Key words: litter trapper, growth form, architectural model, humus collection.

Resumen: La captación de la hojarasca del bosque y la explotación del material en descomposición son estrategias de vida bien conocidas en helechos epifíticos y bromelias tanque. Sólo recientemente, esta estrategia ha sido descubierta en plantas vasculares terrestres, también llamadas plantas captadoras de hojarasca (TLTs). En el bosque lluvioso de Golfo Dulce, TLT fueron encontradas en un elevado número, tanto en su composición específica (en lugares) como por el número de individuos, y obviamente juegan un rol ecológico significativo. En el presente trabajo, se entrega una lista de especies con una clasificación preliminar de modelos arquitectónicos y se describen las variadas adaptaciones morfológicas para capturar la hojarasca. La hojarasca es guiada al centro de la corona o a la base del tallo, donde se acumula y descompone. En algunas especies, las raices adventicias crecen en la hojarasca en descomposición para captar nutrientes, en otras, las plantas se benefician del fluido del tallo rico en nutrientes, obteniendo un beneficio mayor, el enraizamiento de las plantas. Las captadoras de hojarasca representan un atajo en el ciclo de descomposición de la hojarasca y de esta forma una adaptación a los suelos pobres en nutrientes de bosques lluviosos.

Palabras clave: plantas captadoras de hojarasca, forma de crecimiento, modelo arquitectónico, colección de humus.

Introduction

Litter trapping is a well known life and survival strategy of tropical epiphytic ferns (e.g., *Asplenium nidus* and allies, *Platycerium* spp., *Drynaria* spp.) and tank bromeliads (*Vriesea* spp, *Guzmania* spp.). GOEBEL (1889) described this specialised growth form in many paleotropical ferns. Recent studies were conducted by JANSSEN & SCHNEIDER (2005) in Polypodiaceae (*Drynaria*, *Agalaomorpha*), by ELLWOOD (2002) in Aspleniaceae (*Asplenium*), and by BENZING (1989) in tank bromeliads. All these plants compensate for the deficiencies arising from the lack of soil contact by collecting dead leaves, twigs and detritus from the surrounding forest trees. The litter accumulates in their foliage or mantle leaves and decomposes there. Extraction of nutrients takes place through a dense felt of stem-borne roots penetrating into the rotting material which the plant produces.

As recently as the 1980s, the litter-trapping habit has also been recognised in ground-rooted rainforest plants (NG 1980, RAICH 1983, DRESSLER 1985, RICK-

Stapfia **88**,
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Landesmuseen
Neue Serie **80** (2008):
143-154

SON & RICKSON 1986, VASCONCELOS 1990, BERNAL & BALSLEV 1996, ALVAREZ-SANCHEZ & GUEVARA 1999). We call these plants terrestrial litter trappers (TLTs). They represent mainly treelets and palms of the rainforest understorey, and (more rarely) ground herbs. They belong almost exclusively to the angiosperms.

Litter falling from the forest trees is captured by forming a leaf funnel. The decaying material is fixed by the leaf bases, cataphylls or spines curving downwards in the course of growth (ALVAREZ-SANCHEZ & GUEVARA 1999). The collected litter quickly decomposes and nutrient-rich humus is produced (BERNAL & BALSLEV 1996). Shoot-borne roots produced in the crown region indicate the uptake of nutrients from trapped litter. This evidence was first found in the Asian tropics, e.g. in *Agrostistachys longifolia* and *Trigonostemon wetriifolius* (Euphorbiaceae) in Malaysia (NG 1980), later also in Africa (Lower Guinea) in *Coffea magnistipula* (Rubiaceae) (STOFFELEN et al. 1997) and in the Neotropics, e.g. in *Capparis antonensis* (Capparaceae) and *Psychotria dressleri* (Rubiaceae) in Panama (DRESSLER 1985).

TLTs have apparently developed an adaptation to short-cut the common litter fall pathway, thus gaining a competitive advantage over non-collecting plants that depend on nutrient uptake from the soil. Nonetheless, there is some dispute about the significance of litter trapping and nutrient exploitation. In particular, when TLTs do not produce roots penetrating the nutrient traps, nutrient capture is not directly evident and has been questioned (RAICH 1983, DRESSLER 1985). Detailed studies on the decomposition of the trapped litter and the uptake of nutrients by TLTs without shoot-borne roots have been carried out recently by the authors and will be published shortly (WANEK & WEISSENHOFER, in prep.).

Altogether, the diversity, morphology, ecology and ecophysiology of TLTs is still very little known and poorly understood (NG 1980, DRESSLER 1985).

Here we present a list of the species and a classification of the architectural TLT types found so far in the Golfo Dulce region. Moreover, we give a brief description of all TLT species and their devices for litter trapping and discuss the advantages of this specialised growth form.

Study area

The study was conducted in the lowlands of the Golfo Dulce region, mainly in Piedras Blancas and Corcovado National Parks. The Estación Tropical La Gamba (E 257756 m, N 962502 m, altitude 78 m, UTM WGS 84) served as base for most of our studies.

The area has been classified as tropical wet forest (HOLDRIDGE 1967). Details about the vegetation, climate, geology, geography and soils are given in WEBER et al. (2001) and the chapter Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica) of this book.

Sampling

During the period 1997-2007, various field trips were undertaken and all potential terrestrial litter-trapping plants were collected, herbarium specimens were prepared, and the plants were later identified at the Museo Nacional de Costa Rica, San José and at the Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica. All plants were morphologically analysed and the growth patterns found were used to define basic architectural types. Further studies were performed to investigate the mass (weight) of collected litter, time of decomposition, absorption of nutrients provided by the rotten material, growth rates, leaf position, collection devices, presence/absence of adventitious roots in the leaf crown etc. Moreover, we studied and documented the frequency of the TLT species in different ecological niches.

Species diversity

So far, 24 TLT species in 21 genera and 10 angiosperm families have been collected in the Golfo Dulce region (Table 1). The most prominent group are the monocotyledons with 15 species, comprising 67% of all identified TLT species (see Fig. 1). Within this group, the palms are the most important family, with 8 species (34%) in 8 different genera. The high representation is apparently due to the commonness of the monaxial and leaf-tufted growth form ("Schopfbäumchen") which a priori facilitates litter collection. The other monocotyledonous families with TLT plants are the Araceae (1 sp.), Bromeliaceae (1 sp.), Cyclanthaceae (3 spp.), Cyperaceae (2 spp.) and Marantaceae (several species).

The dicotyledons are represented by 8 species (comprising 33% of TLT species) in 6 genera and 4 families. Here, the Rubiaceae are the most important family, with 4 species in 2 genera. The other represented families are the Myrsinaceae (2 spp.), Sabiaceae (1 sp.) and Theophrastaceae (1 sp.).

Growth forms (plant architecture)

Until now, no worldwide or regional classification of the growth forms of TLTs exists. DRESSLER (1985) distinguished two main types, corresponding to type 2 and 3 in the present classification. WEISSENHOFER & WEBER

(1999) recognised three types. Since then, new observations and data have been obtained which allow the establishment of a new and more detailed classification of the TLTs found in the Golfo Dulce region.

Type 1. Low, large-leaved ground herbs forming a leaf funnel. This type is found only in the monocotyledons (Araceae: *Spathiphyllum wendlandii*; Bromeliaceae: *Chevaliera magdalenae*; Cyclanthaceae: *Asplundia alata*, *Asplundia pittierii*, *Sphaeradenia acutitepala*; Cyperaceae: e.g., *Becquerelia cymosa*, *Diplasia karatifolia*), Marantaceae (several species) but not in palms (plate 1 and 2). Ca. 33% of the TLT species represented in the Golfo Dulce belong to this type. Adventitious roots growing into the rotting litter mass are always present. Sometimes the roots grow straight upwards (negativly geotropic), e.g., in *Spathiphyllum wendlandii*.

Type 2. Treelets and palms (rarely herbs) with a single, unbranched stem and a large tuft of narrow,

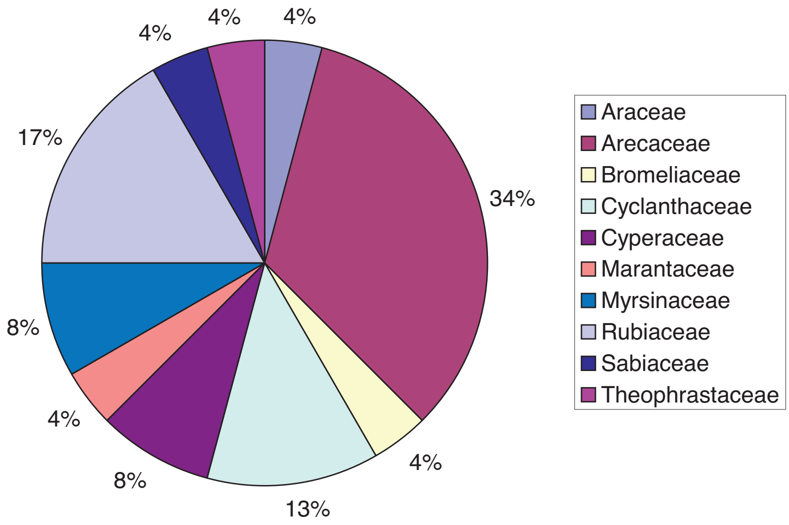


Fig. 1: Percentage of species and families of TLTs collected so far in the Golfo Dulce region.

Table 1: List of terrestrial litter–trapping plant species (angiosperms) presently known from the Piedras Blancas National Park, Costa Rica.

Nr.	Family	Species	Growth habit	TLT type	Roots in the humus accumulation	Habitat
1	Araceae	*Spathiphyllum wendlandii* Schott	herb	1	always present	ravine forest
2	Arecaceae	*Asterogyne martiana* (H. Wendl.) H. Wendl. ex Hemsl.	palm	2	rarely present	ravine to slope forest
3	Arecaceae	*Calyptrogyne ghiesbreghtiana* (Linden & H. Wendl.) H. Wendl.	palm	2	lacking	ravine to slope forest
4	Arecaceae	*Elaeis oleifera* (Kunth) Cortés	palm	2	commonly present	wet areas along streams
5	Arecaceae	*Geonoma cuneata* H. Wendl. ex Spruce	palm	2	lacking	ridge forest
6	Arecaceae	*Oenocarpus mapora* H. Karst.	palm	4	always present	ridge forest
7	Arecaceae	*Prestoea decurrens* (H. Wendl. Ex Burret) H. E. Moore	palm	4	commonly present	ravine forest
8	Arecaceae	*Raphia taedigera* (Mart.) Mart.	palm	2	commonly present	swampy areas near the sea
9	Arecaceae	*Welfia regia Mast.*	palm	2	lacking	ravine to ridge forest
10	Bromeliaceae	*Chevaliera magdalenae* André (André ex Baker)	herb	1	always present	ravine to ridge forest, gaps
11	Cyclanthaceae	*Asplundia alata* Harling	herb	1	commonly present	ravine to slope forest
12	Cyclanthaceae	*Asplundia pittieri* (Woodson) Harling	herb	1	commonly present	slope forest
13	Cyclanthaceae	*Sphaeradenia acutitepala* Harling	herb	1	always present	slope forest
14	Cyperaceae	*Becquerelia cymosa* Brongn.	herb	1	always present	ridge forest, gaps
15	Cyperaceae	*Diplasia karatifolia* Rich.	herb	1	always present	ridge forest, gaps
16	Marantaceae	*Calathea* spp.	herb	1	lacking	ravine forest
17	Myrsinaceae	*Ardisia pittieri* Mez	treelet	3	lacking	ravine to slope forest
18	Myrsinaceae	*Cybianthus schlimii* (Hook. f.) G. Agostini	treelet	2	lacking	ravine to slope forest
19	Rubiaceae	*Pentagonia macrophylla* Benth.	treelet	5	lacking	ravine forest
20	Rubiaceae	*Pentagonia wendlandii* Hook.	treelet	5	commonly present	ravine forest
21	Rubiaceae	*Psychotria alfaroana* Standl.	treelet	5	lacking	ravine forest
22	Rubiaceae	*Psychotria chitariana* Dwyer & C.W. Ham.	treelet	5	lacking	ravine forest
23	Sabiaceae	*Meliosma donnelsmithii* Urb.	treelet	2	lacking	ravine to slope forest
24	Theophrastaceae	*Clavija costaricana* Pittier	treelet	2	rarely present	ravine to slope forest

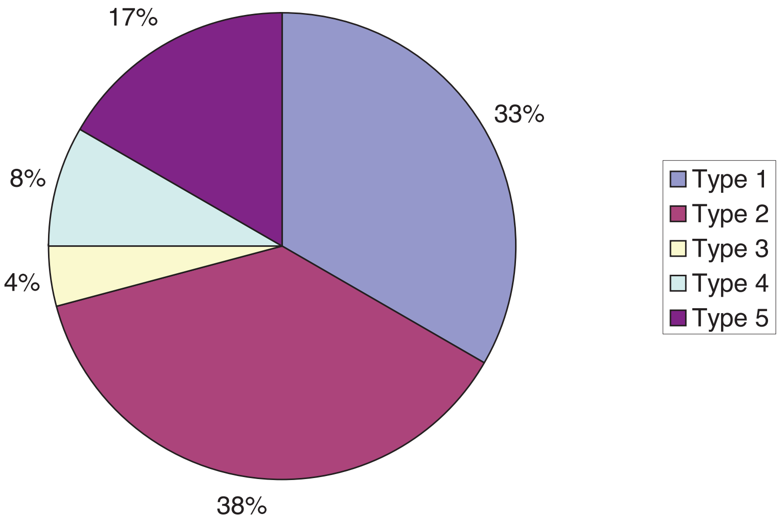
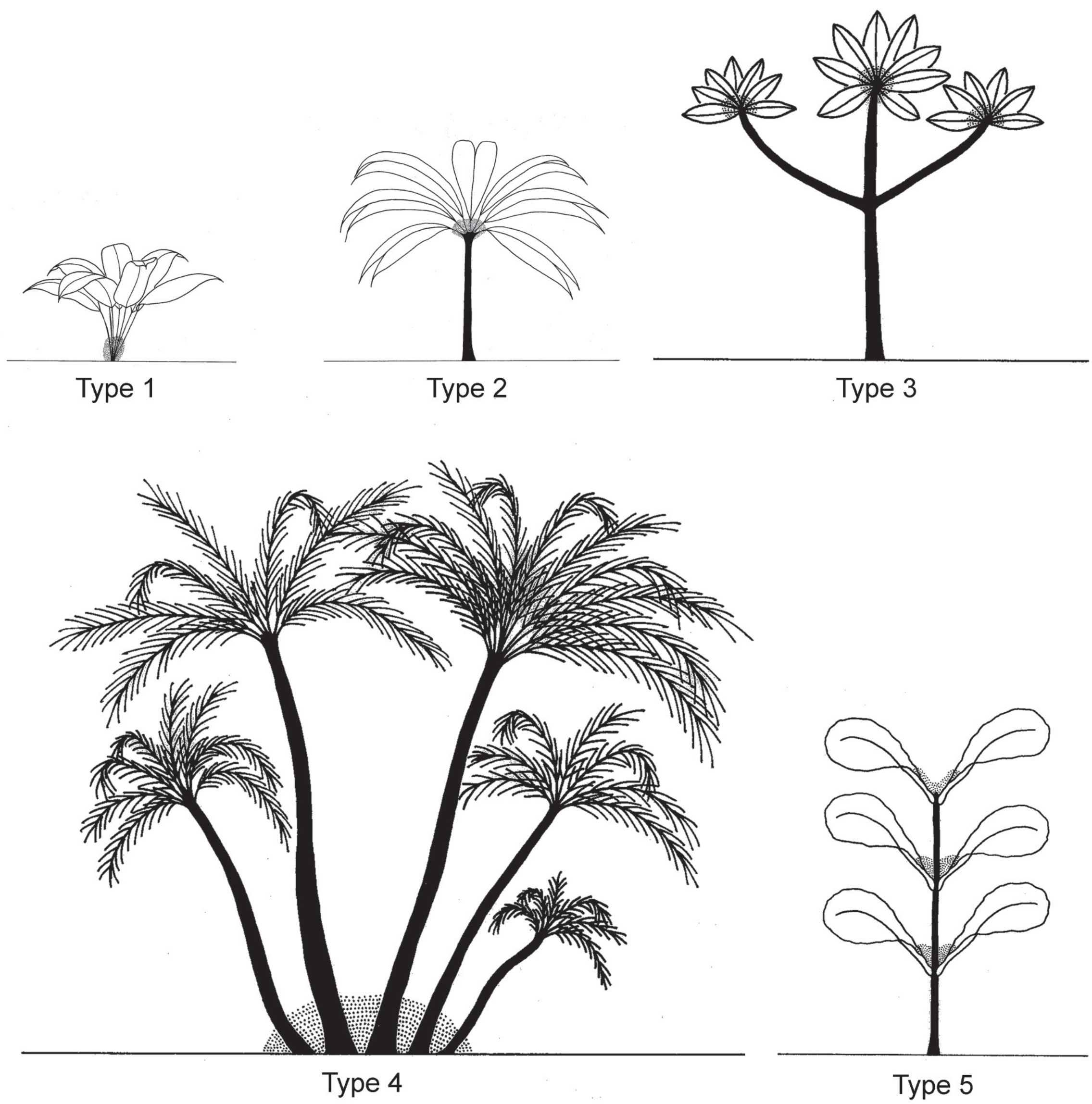


Fig. 2: Percentage of growth patterns (architectural types) represented in the TLT species found so far in the Golfo Dulce area.

(ob)lanceolate leaves on top. We call it a monoaxial tufted treelet corresponding to the German "Schopfbäumchen" (plate 1 and 3). This is the most common type (38%) and represented in various monocotyledonous and dicotyledonous plant families. Shoot-borne roots in the crown zone of the species are sometimes developed

Type 3. Branched shrubs with each branch bearing a litter-collecting leaf tuft (plate 1 and 4). This type is rare (4%) and has so far been found in the region only in *Ardisia pittieri* (Myrsinaceae). Two other species belonging to this type, *Erythrochiton gymnanthus* (Rutaceae) and *Capparis antonensis* (Capparaceae), occur outside of the Golfo Dulce, in the Central Pacific region of Costa Rica (Parque Nacional Carara) and at Cerro Anton (Panama), respectively. Adventitious roots are rare in this type and have so far only been found in *Capparis antonensis*.

Plate 1: The five TLT types that have been discovered so far. For details see text.



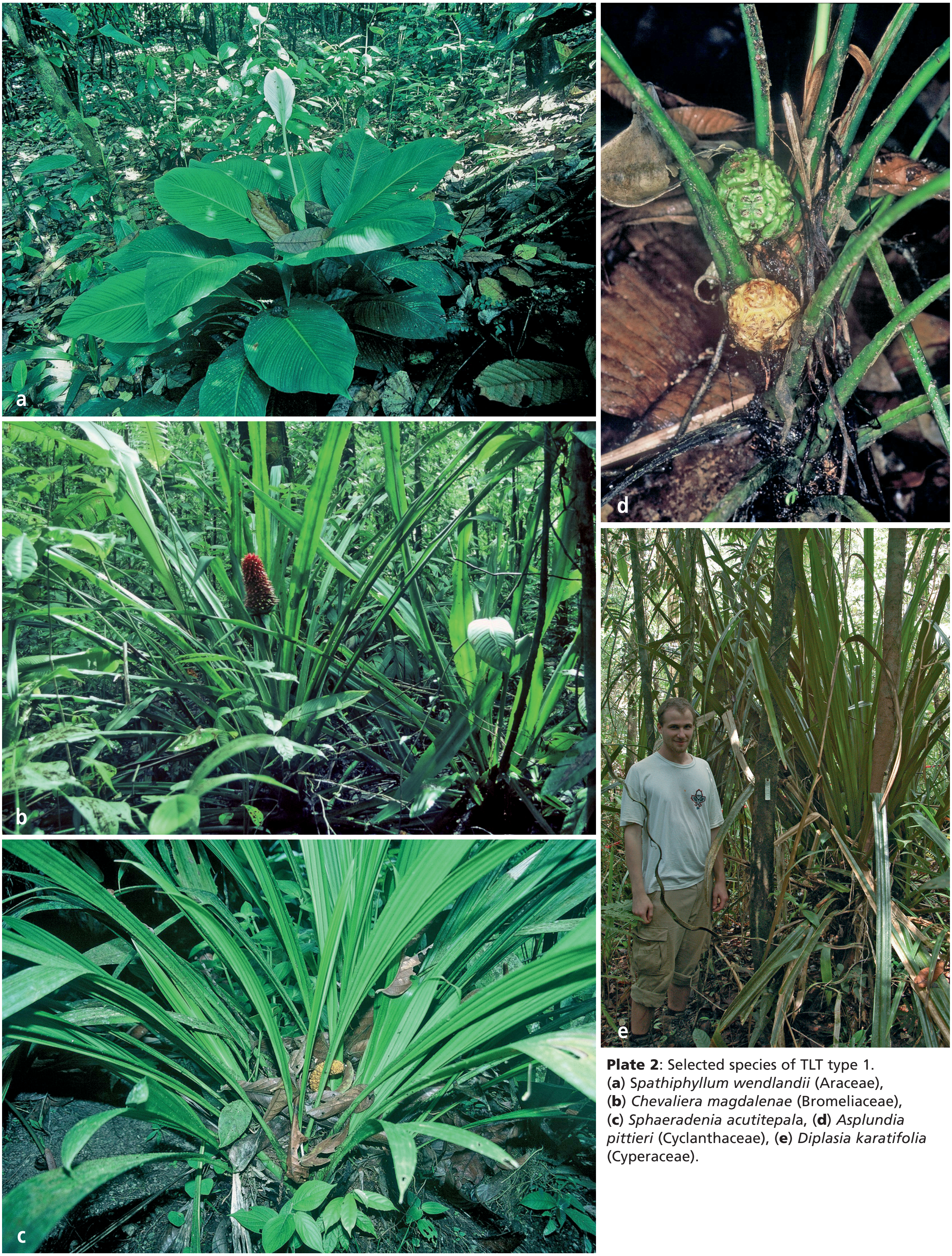


Plate 2: Selected species of TLT type 1. (**a**) *Spathiphyllum wendlandii* (Araceae), (**b**) *Chevaliera magdalenae* (Bromeliaceae), (**c**) *Sphaeradenia acutitepala*, (**d**) *Asplundia pittieri* (Cyclanthaceae), (**e**) *Diplasia karatifolia* (Cyperaceae).

Plate 3: Selected species of TLT type 2. (**a**) *Asterogyne martiana*, (**b**) *Elaeis oleifera*, (**c**, **d**) *Welfia regia* (Arecaceae), (**e**) *Clavija costaricana* (Theophrastaceae), (**f**) *Cybianthus schlimii* (Myrsinaceae).

Plate 4: Selected species of TLT type 3-5. (**a**) *Ardisia pittieri* (Myrsinaceae), a member of the rare TLT type 3. (**b**) *Oenocarpus mapora*, (Arecaceae) of TLT type 4. (**c**) *Pentagonia wendlandii* and (**d**) *Psychotria chitariana* (Rubiaceae) of TLT type 5.

Type 4. Clump-forming palms that produce a large "hyperfunnel" with all their stems and apical leaf crowns (plate 1 and 4). This type was recently discovered in two palms in the Golfo Dulce region, *Geonoma congesta* and *Oenocarpus mapora*, that is in 8% of all TLTs. We have the impression that this type is more common in other regions, but studies are lacking so far. The litter accumulates at the base of the stems, close to the ground. Adventitious ground roots growing into the humus accumulation are consistently produced.

Type 5. Treelets, shrubs and subshrubs collecting litter in the axils of spaced leaves. These plants often have broad leaf blades and leaf bases forming collection cups which facilitate litter accumulation and decomposition (plate 1 and 4). Four species (17%), all in the family Rubiaceae, belong to this type. Until now, no crown roots have been found. The plants apparently gain profit from the nutrient-rich rainwater flowing along the stem into the soil, from where it is taken up by ground roots. A plant of the same type, *Coffea magnistipulata* (Rubiaceae), is known from Lower Guinea (Africa), which, however, produces adventitious roots in the crown region and along the stem. They grow into the decomposing litter mass and thus present direct evidence of nutrient uptake (STOFFELEN et al. 1997).

Ecology and habitats of TLTs

In the Golfo Dulce region, TLTs occur in various forest sites, most of them being confined to primary forest. Only a few species (e.g., Cyperaceae: *Becquerelia cymosa*, *Diplasia caratifolia*; Bromeliaceae: *Chevaliera mag-*

dalenae) grow in old secondary forest and in small to medium-sized gaps. TLTs are fairly common in valley bottoms and ravines (Table 1), where microclimatic conditions are very humid throughout the year and promote the decomposition of the fixed organic material (without any soil contact). In total, 16 of the 24 collected species occur at wet sites, 8 of which are confined to ravine forest. In contrast, only 4 species prefer drier and more open sites of the ridge forest.

It is conspicuous that only TLT type 1 and 4 have been found at drier sites. This pattern has also been observed in other regions in the Neotropics (Province Guanacaste, Venezuela, pers. observ.) and so far, no other TLT types have been found at the more xeric sites. These plants collect the litter preferentially at the stem base, where microclimatic conditions are more balanced throughout the year (with considerable moisture even in the dry season) and thus facilitate decomposition. In such plants, decomposition would be impossible without soil contact.

Roots in the humus accumulation

The presence of adventitious roots in the humus accumulation is a direct indication of nutrient uptake. In total, 58% (14 of 24 species) of the TLTs produce adventitious roots in the crown region or at the ground level. Only in 9 species were such roots never found.

Two different groups of adventitious roots can be distinguished: (1) roots at or closely above the ground level, and (2) roots in the crown (leaf) region. The first type is characteristic of monocotyledons, especially of herbs of TLT type 1 and for palms of TLT type 4.

In contrast, adventitious roots in the crown region of woody plants are rare (GILL 1969), however, they are found occasionally both in monocotyledonous and dicotyledonous TLTs. In total, we found 4 species with crown roots of the relevant TLT types 2, 3 and 5, making 35%. These roots are a specific and probably more specialised adaption to litter trapping than adventitious roots on the ground. The roots are important for direct nutrient uptake and also for retaining the mass of humus which could easily be washed out by heavy rainfalls.

This leaves the question of what benefit TLT species that never produce adventitious roots in the humus mass derive.

So far, the general opinion was that TLTs without such roots may take up nutrients from the collected litter only through the nutrient-rich stem flow (RAICH 1983). This would mean that the regular litter fall pathway is cut short and that plants may gain a competitive advantage over non-collecting plants which rely solely on nutrient inputs to soil solution by litter and soil organic matter decomposition. However, recent observations show that TLTs without crown roots seem to take up nutrients with organs other than roots, e.g. leaves, cataphylls, and stem surface. Detailed studies on the decomposition of the trapped litter and the uptake of nutrients with and without shoot-borne roots were conducted by the authors and will be published shortly (WANEK & WEISSENHOFER, in prep).

TLTs and animals

The litter and humus accumulations contain a very rich fauna (VASCONCELOS 1990, DRESSLER 1985) which probably aids in litter decomposition. We found several animal groups in the litter traps such as Annelida, Crustacea (Isopoda), Diplopoda, Arachnida (various groups of spiders and scorpions), Collembola, Coleoptera, Hemiptera, Lepidoptera, Diptera, Hymenoptera, snakes and reptiles (*Anolis* sp.), which used the humus accumulation for nesting, prey or food. Ants were nearly omnipresent and most of them showed aggressive behaviour. In *Clavija costaricana*, 10 out of 15 litter traps were found to be inhabited by various species of ants. We observed that plants inhabited by ants were free or nearly free from epiphyllous mosses, liverworts or lichens. The ants apparently protect the leaves against herbivores and epiphylls.

Brief descriptions of the TLT species found in the Golfo Dulce region

Araceae

Spathiphyllum wendlandii. Terrestrial rhizomatous herb, up to 80 cm tall. TLT type 1. The elliptic leaves form a leaf funnel, in which the litter is collected. The decomposed organic material is fixed in the centre of the rosette, mainly by the leaf sheaths. Adventitious roots grow into the humus mass and into the leaf sheaths (with negative geotropism) where fine litter accumulates. The species occurs in wet forests from Costa Rica to Panama. In the study area, we found *S. wendlandii* mostly in colonies in swampy places in the wettest parts of the forest, mainly along rivers in ravine and riverine forests.

Arecaceae

Asterogyne martiana. Solitary understorey palm, growing up to 2 m tall. TLT type 2. Litter is collected by the large, apically bifid leaves and decomposed at the leaf base. This widespread species occurs in lowland rainforest, with a geographical range from Central America (Belize) to western Colombia and Ecuador. In the study area, *A. martiana* grows predominantly on valley bottoms and on poorly-drained slopes or terraces.

Calyptrogyne ghiesbreghtiana. Solitary and short-stemmed understorey palm, to 2 m tall. TLT type 2. Litter is collected as in *Asterogyne martiana*. The species is native to Central America, occurring mainly on the Carribean coast. On the Pacific coast, it has only been collected in the Guanacaste Province and in the Golfo Dulce region, where it grows in primary ravine and slope forest.

Elaeis oleifera. A relative of the African oil palm, with a creeping stem to 6 m long but not exceeding 2 m in height. TLT type 2. The persisting leaf bases decompose together with the collected litter at the top. Adventitious roots grow into the humus mass. The species is native to Central and South America. In the Golfo Dulce region, specimens have been found in open areas along meandering streams on poorly drained, often inundated soils.

Geonoma cuneata. Solitary (rarely clustered) understorey palm, up to 2 m tall. TLT type 2. The litter is collected as in *Asterogyne martiana*, but no shoot-borne adventitious roots have so far been found. It is a widespread (Central to South America) and extremely variable species. In southern Costa Rica, the species is fairly common on well drained soils (slopes) in primary forest.

Oenocarpus mapora. An arborescent and clustered palm of the mid-canopy, growing up to 20 m tall. TLT type 4. Litter is collected by the clustered crowns ("hypercrowns") and funneled to the ground, where adventitious roots take up the nutrients. The species is distributed from Costa Rica to western South America and northern Bolivia. In the Golfo Dulce region, it occurs mainly in primary ridge forest.

Prestoea decurrens. Clump-forming arborescent palm, up to 12 m tall. TLT type 4. Litter is collected as in *Oenocarpus mapora* and adventitious roots grow into the humus mass. The species is distributed from Nicaragua to the Pacific lowlands of Colombia and Ecuador. In the Golfo Dulce, it occurs in ravines and very wet areas of primary forest.

Raphia taedigera. Clump forming palm, up to 12 m tall, with stems of unequal age and persistent leaf bases. TLT type 2. Litter is trapped with leaf funnels and guided to the crown centre and leaf bases, where it decomposes together with the rotten leaf bases, forming a mat around the trunk. Adventitious roots grow negatively geotropically inside the humus mass, fix the litter and take up the nutrients. The species is distributed from Nicaragua to NW Colombia and in the estuary of the Amazon, where it prefers waterlogged soils in inundated areas. In the Golfo Dulce region, it occurs in swampy areas, mainly between Sierpe and Los Mogos (Yolillo forest).

Welfia regia. Solitary palm, up to 20 m tall, with a mass of adventitious roots at the base. TLT type 2. Litter is trapped as in *Raphia taedigera*, and no adventitious roots have been found. It is remarkable that young and stemless plants also collect litter. The species is distributed from Honduras to Colombia and Ecuador. In the Golfo Dulce, it occurs mainly in primary forest on slopes and ridges, but was also found in ravines.

Bromeliaceae

Chevaliera magdalenae. Tank bromeliad, growing up to 1 m tall. TLT type 1. Litter is intercepted by the leaves arranged in a rosette and guided to the centre, where adventitious roots grow into the humus. The species is distributed from Belize to Colombia, Ecuador and Venezuela. In the Golfo Dulce region, we have collected specimens at a wide ecological range of sites, from very humid places near rivers (Río Sardinal), to drier ridges and also near the beach (Corcovado National Park, near Río Madrigal).

Cyclanthaceae

Asplundia alata. Short-stemmed terrestrial plant with bifid leaves (up to 110 cm long) arranged in a rosette. TLT type 1. Litter is collected in the centre of the rosette where adventitious roots grow into the humus mass. The species is known from Costa Rica and Panama. In the Golfo Dulce region, the species was observed and collected in ravine and ridge forest.

Asplundia pittieri. Terrestrial herb with bifid leaves (up to 22-35 cm long) arranged in a rosette. TLT type 1. Litter is collected in the centre of the rosette. Adventitious roots growing in the litter zone were observed. The species is distributed from Costa Rica to Colombia. In the Golfo Dulce region, it is a common understorey plant of primary slope forest.

Sphaeradenia acutitepala. Short-stemmed herb with bifid leaves (up to 140 cm long) arranged in a rosette. TLT type 1. Normally, *S. acutitepala* grows as an epiphyte, but we have also seen plants growing on the forest floor in the region. Litter accumulates in the centre near the base of the plant where adventitious roots grow inside the humus mass. The species occurs in wet forests from Nicaragua to northern Colombia. In the Golfo Dulce, it is mainly found on slopes.

Cyperaceae

Becquerelia cymosa. Herb with solitary erect culms up to 150 cm tall and leaves up to 150 cm long. TLT type 1. The litter is trapped with the long and thin leaves and transported to the centre near the ground, where it decomposes. Adventitious roots grow into the humus accumulation. The species is distributed from

Nicaragua to southern Brazil. In the Golfo Dulce region, it occurs at drier sites, mainly at ridges in primary and secondary forest, sometimes also in gaps.

Diplasia karatifolia. Tall perennial herbs with leaves up to 150 cm long. TLT type 1. Litter is trapped and adventitious roots are formed as in *Becquerelia cymosa*. The species is widespread, ranging from Costa Rica to Peru, Bolivia and Brazil. In the Golfo Dulce region, it grows mainly at drier sites.

Marantaceae

***Calathea* spp.** Erect, rosulate forest herbs, mostly 1-2 m tall. TLT type 1. *Calathea* is the largest genus in the Marantaceae with 300 sp. in the Neotropics and 16 in the Golfo Dulce region. Here, we found several species which occasionally trap litter with their large, distichously or spirally arranged leaves, guiding the organic material to the ramifications of the plants. So far, no adventitious roots have been found.

Myrsinaceae

Ardisia pittieri. Small treelet up to 6 m tall. TLT type 3. The leaves are cuneate-oblanceolate to elliptic-oblong, 15-60 cm long and clustered at the end of the branchlets where the litter is collected. The species is distributed from Costa Rica to Panama; in the Golfo Dulce region, it occurs in primary forest, growing in ravine or ridge forest.

Cybianthus schlimii. Shrub or small treelet up to 2 m tall. TLT type 2. The leaves are up to 55 cm long, 15 cm wide and apically clustered, forming a distinct funnel. This is a widely distributed species (Costa Rica to Colombia, Ecuador and Peru), but was rarely collected in the study area where it grows in primary ravine or ridge forest.

Rubiaceae

Pentagonia wendlandii. Small treelet, up to 3(4) m tall. TLT type 5. Litter is collected with distally clustered large obovate to oblong leaves. The litter is fixed by the cuneate and rounded leaf bases and the persistent stipules. This species occurs in lowland primary rainforests, ranging from Costa Rica to Central Panama. In the study area, *P. wendlandii* prefers humid sites of primary and late secondary forest.

Pentagonia macrophylla. Unbranched (rarely branched) treelet, 1-5 m tall. TLT type 5. Litter is collected as in *P. wendlandii*. This ecologically very variable species is distributed from Costa Rica to Panama, Colombia, Ecuador and Peru from 0-1.700 m above sea level (a.s.l.). In the Golfo Dulce region, *P. macrophylla* grows in primary and late secondary ravine forest.

Psychotria alfaroana. A very small treelet, up to 0.6 m tall. TLT type 5. Small litter fragments adhere to the midvein and leaf axils. The species ranges from Costa Rica (Guanacaste) to Panama (Bocas del Torro) and Colombia. In the study area, we collected the species only in wet ravine forest.

Psychotria chitariana. This small treelet grows up to 5 m tall. TLT type 5. Debris is accumulated in the leaf axils of the large leaves which are up to 35 cm long and 15 cm broad. The species is known only from very wet sites in Costa Rica (0-800 m a.s.l.) on the Atlantic and Pacific slopes. In the Golfo Dulce region, it was observed only in ravine forest.

Sabiaceae

Meliosma donnelsmithii. This is a small tree up to 8 m tall. TLT type 2. Litter is accumulated and fixed in the centre of the crown region by the large subsessile leaves and auriculate leaf bases. The species is distributed from Nicaragua to Panama on the Atlantic and Pacific slope. In the Golfo Dulce region, it is found in ravine and slope forests.

Theophrastaceae

Clavija costaricana. Small treelet up to 5 m tall. TLT type 2. Litter is collected by the terminal tufts of large (up to 120 cm long and up to 23 cm broad) oblanceolate and glabrous leaf blades. The organic material is decomposed at the base of the leaves and fixed by small, stiff cataphylls. Adventitious roots were rarely found. *C. costaricana* occurs only in wet or moist primary forest. Its distribution is from Southern Nicaragua to northwestern Colombia. In the study area, it is found only in the most humid parts such as ravines and rarely on slopes.

Conclusions

Litter trapping of terrestrial plants has only recently been discovered and is still a poorly known life strategy of tropical plants. Terrestrial litter trappers have evolved in various taxonomic groups, in both the monocotyledons and the dicotyledons. TLTs exhibit different degrees of adaptation with regard to the collection and retention of litter and to nutrient uptake from the decomposing organic material. Direct evidence for nutrient uptake can be found in those species which (in the leaf crown region!) produce adventitious roots growing into the litter accumulation (e.g., *Oenocarpus mapora*, *Chevaliera magdalenae*, *Sphaeradenia acutitepala* etc.). The lack of such roots (e.g., in *Geonoma cuneata*, *Calathea* spp., *Ardisia pittieri* etc.; see Table 1 and species descriptions), however, cannot be taken as an argument for a functional insignificance of the observed litter trapping. Nutrient uptake may occur by the stem or other aerial parts of the plants (e.g., leaf bases and stipules in *Pentagonia wendlandii*, cataphylls and leaf bases in *Clavija costaricana*) or by ground roots which absorb the nutrients from rainwater (stem flow) funneling through the nutrient-rich litter accumulation down the stem towards the stembase.

The ecological significance is evident. TLTs are almost exclusively found in rainforests and thus in plant communities that establish on soils which are extremely poor in nutrients. By obtaining additional nutrients via the exploitation of decaying organic matter, they avoid competition for nutrients with other ground-rooted plants that depend solely on nutrient uptake from the soil. Therefore, they may gain a competitive advantage over non-litter trapping ground-rooted plants and in places outcompete them.

The high abundance and species richness (24 species in 21 genera and 10 families) of TLTs in the Golfo Dulce region is directly associated with high mean annual precipitation (5.800 mm) and temperature (25.2°C). In general, perhumid conditions allow and promote the litter trapping habit: the intercepted litter remains moist during most of the year, thereby facilitating decomposition. At humid sites, decomposition of the organic material is therefore possible in the crown region of the TLTs, i.e. distant from the soil and disconnected from the large soil water reservoir. For the same reason, most of the litter-trapping species and individuals are found in the understorey of ravine forests. Here, the species diversity is higher than in adjacent and somewhat drier sites such as in slope or ridge forests.

However, microclimatic conditions vary noticeably within the area and, in general, ravines and ravine forests are more humid than ridges and slopes. TLT types change with microclimatic conditions and each TLT type occupies its own niche. At the wettest sites, TLT species of all architectural types can be found whereas in the drier sites (e.g., ridge forest) the TLTs belong mostly to the types collecting litter at the stem base (especially TLT type 1). This is due to the somewhat drier microclimate during February and March which results in drought stress within the canopies effectively preventing litter decomposition in the crowns. On the other hand, close to the ground, the microclimate is humid enough to allow litter decomposition during the dry months.

The most conspicuous and probably best adapted TLTs in the Golfo Dulce region are *Asterogyne martiana*, *Clavija costaricana* and *Pentagonia macrophylla*. In the understorey of ravines and ravine forests, they can form almost pure stands.

It is remarkable that no investigation has so far been carried out on the diversity, ecology and abundance of litter-trapping plants in other regions in the tropics. Therefore, the question arises whether TLTs have not been recognised as a special plant functional group or whether they are less significant or absent in other regions. From our personal observations in the Golfo Dulce region, we propose that the litter-trapping habit is a common and important strategy in wet forests throughout the tropics, but that it has not been fully recognised as a significant ecological adaptation to nutrient-poor ecosystems.

Acknowledgement

Many thanks go to Tamara Zhuber for the line drawings of plate 1.

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