From Forest Floor To The Canopy:
Life History Of
Secondary Hemiepiphytes
(*Heteropsis* Species)
In The Colombian Amazon

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Cover: Painting by Maestro ***Fabian Moreno***, Muinane indigenous (FamGo Moreno G) 2009.

Back: The path that a *Heteropsis* seedling has go through, once it germinates.

Designed and Photos by: María Paula Balcázar-Vargas

FROM FOREST FLOOR TO THE CANOPY: LIFE HISTORY OF SECONDARY HEMIEPIPHYTES (*HETEROPSIS* SPECIES) IN THE COLOMBIAN AMAZON

VAN BOSBODEM TOT DE KROON: LEVENSGESCHIEDENIS VAN SECUNDAIRE HEMIEPIPHYTEN (*HETEROPSIS* SOORTEN) IN DE COLOMBIAANSE AMAZONE

(met een samenvatting in het Nederlands)

DESDE EL SUELO HASTA EL DOSEL DEL BOSQUE: LA HISTORIA DE VIDA DE LAS HEMIEPÍFITAS SECUNDARIAS (*HETEROPSIS* SPP.) EN LA AMAZONIA COLOMBIANA

(con resumen en español)

Proefschrift

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door
María Paula Balcázar Vargas

geboren op 22 September te Bogotá, Colombia

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Aan Thijs en Vincent
y mi mami, María Teresa

Joaquin S. Lavado (Quino). 1990. Mafalda 11. Editorial La Oveja Negra Ltda. ISBN:958-061937-9.

Although in the Quino's cartoon appears a liana not a hemiepiphyte, actually the philosophical problem is almost the same.

A pesar que en la caricature de Quino aparece una liana y no una hemiepífita, en realidad el problema filosófico es casi el mismo.

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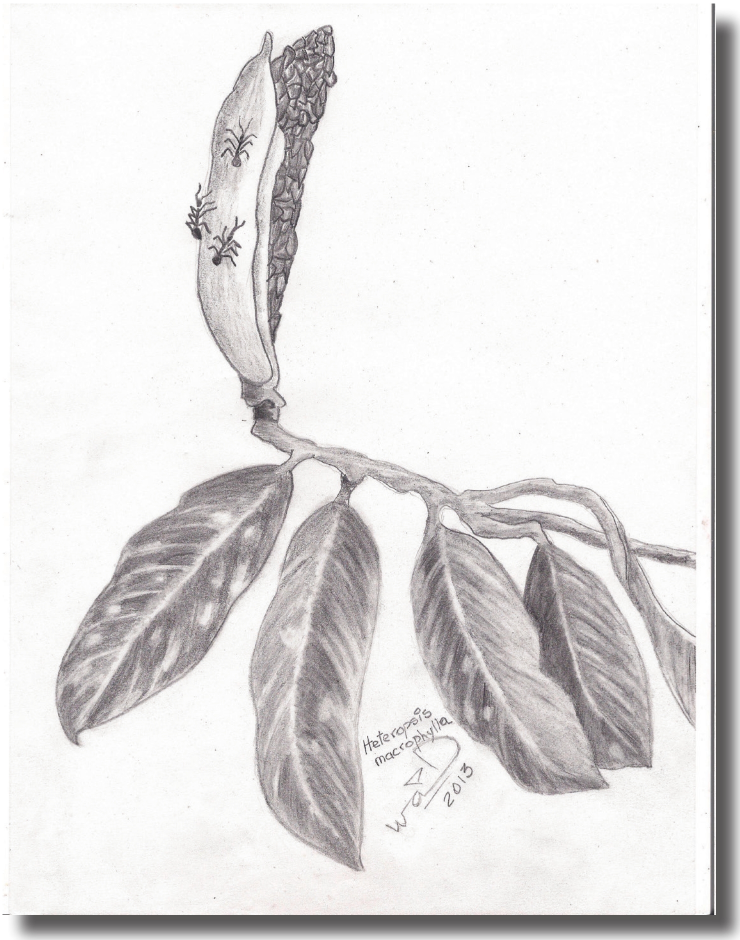


Drawing of *Heteropsis macrophylla* with some ants (Drawing by Maria Teresa Vargas-Paz).

Snippet Huitoto song,

……”jufubi yubak+ nagema jiza k+r+ga+ niyena k+r+ona at+, uziona at+”...... (Huitoto m+n+ka)

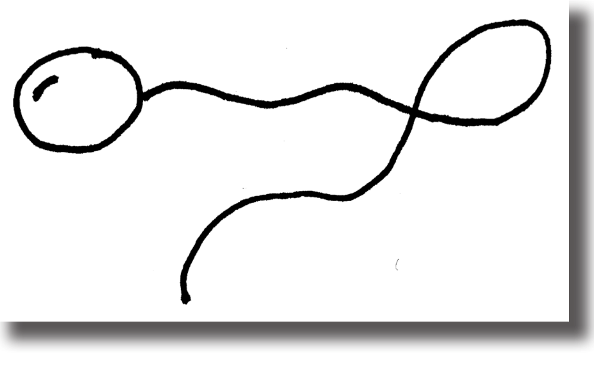
……”Para tejer el canasto para la hija del dueño del baile de la fruta traigan el bejuco *Heteropsis flexuosa* y *Heteropsis macrophylla*”...... (Español).

……”To weave a basket for the owner’s daughter fruit dance bring the vine *Heteropsis flexuosa* and *Heteropsis macrophylla*”...... (English).

Ever Kuiro (Huitoto) from La Chorrera, Amazonas Colombia.

Chapter 1

Introduction



Introduction

THE LIFE CYCLE AND DIVERSITY OF HEMIEPIPHYTES

Climbing plants such as vines, lianas, and secondary hemiepiphytes are typical and important components of tropical forests. Lianas alone can represent up to 25 percent of the vascular flora (Gentry 1991, Nabe-Nielsen 2001, Schnitzer & Bongers 2002). The species diversity of climbing plants in the tropics is high, with over 8000 species of vines and lianas (Gentry 1991), and about 700 to 1000 species of secondary hemiepiphytes (Croat 1988, Williams-Linera & Lawton 1995), represented by several genera of the Araceae, Cyclanthaceae and Marcgraviaceae (Williams-Linera and Lawton 1995).

In contrast to true epiphytes, which spend their entire life on tree branches or trunks without touching the soil (Benzing, 1990), hemiepiphytes maintain soil contact for at least part of their life by means of aerial roots. Primary hemiepiphytes start their life as epiphytes, germinating on a host tree and sending down aerial roots to the ground to take up nutrients (Benzing 1990, Putz & Holbrook 1986). Some primary hemiepiphytes can strangle or kill their host (e.g., *Clusia* spp., *Ficus* spp.); others never do so (e.g., *Philodendron* spp.) On the other hand, secondary hemiepiphytes begin their life as seed on the forest floor. Seedlings of some species (e.g., *Heteropsis*) produce a leafless stem after germinating on the forest floor that moves away from the germination spot. When a host is found, the plant climbs up, attaching itself with adventitious anchoring roots (Wilder 1992, Romero 1994). Once attached, a second type of adventitious roots is produced – absorbing roots – which sprout from the orthotropic stem (shoot or stem growing vertically) and grow downwards. These roots take up water and nutrients from the soil. Once the absorbing roots are functional, the lower part of the stem dies and the plant loses the initial connection with the forest floor and the remains of the seed. Next, it produces plagiotropic branches (horizontal branches bearing leaves in planes along each axis) and more absorbing roots. In this process, the lower parts of the stem senesce together with the lowest roots (Putz & Holbrook 1986, Plowden et al. 2003; Fig. 1).

Other secondary hemiepiphytes, such as species in the genera *Philodendron* and *Monstera* (Araceae) and *Asplundia* (Cyclanthaceae) begin their life rooting in the soil and climbing up a host or phorophyte (a term applied to plants on which an epiphyte resides, Moffett 2000), but afterwards their old roots degenerate and they become true epiphytes. They have been classified as secondary hemiepiphytes, but this is not convincing as they are in fact secondary epiphytes. In some cases they even form aerial adventitious roots again that hang down like curtains and establish contact with the ground for a second time. Thus, secondary hemiepiphytes then become primary hemiepiphytes (Lüttge 2008).

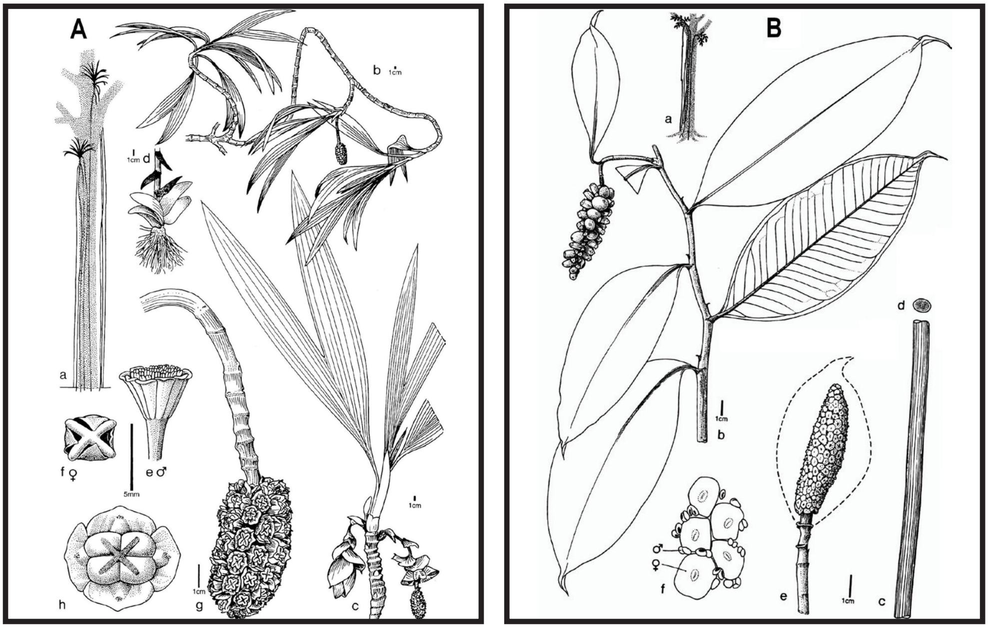


Figure 1. Two species of Neotropical secondary hemiepiphytes. **A) *Thoracocarpus bissectus* (Vell.) Harling (Cyclanthaceae)**. a. habit; b. fruiting branch; c. branch with young flowering spadix (l) and fruiting spadix (r); d. flowering spadix showing bracts and staminoides; e. male flower; f. female flower; g. fruiting spadix; h. fruit. **B) *Heteropsis flexuosa* (Kunth) G.S. Bunting (Araceae)**. a. habit; b. fruiting branch; c and d. aerial root; e. flowering spadix, showing position of the spathe; f. flowers, showing stamens surrounding ovaries and a central style. (Drawing made by Hendrik Rypkema, National Herbarium of the Netherlands. Reproduced from and with permission of Tinde van Andel 2000b).

Unlike holoepiphytes and primary hemiepiphytes, which germinate and grow in the canopy, most of the secondary hemiepiphytes germinate and grow under dark conditions in the mature forest. For those species, light availability increases gradually with height. However, some hemiepiphytic aroids are able to grow in secondary forests and in abandoned agricultural fields (Barthlott et al. 2001, Benavidez et al. 2006). Some authors have referred to secondary hemiepiphytes with different names (nomadic vine, Moffett 2000; pseudo-epiphytes, Schimper 1898). Here I follow the terminology used by Williams-Linera & Lawton (1995).

Life History Strategy, Growing Conditions And Adaptations Of Secondary Hemiepiphytes

Terrestrial and canopy environments vary profoundly in terms of water, light, and nutrient supply (Putz & Holbrook 1986, 1989; Benzing 1990; Williams-Linera & Lawton 1995; Mulkey et al. 1996; Zotz & Andrade 2002). Epiphytic habits require a set of physiological, anatomical and morphological adaptations of plants in order to survive in the harsh canopy environment (Williams-Linera & Lawton 1995). Although epiphytic growth may provide an advantage for access to light and sometimes to nutrients (Nadkarni 1984, Putz & Holbrook 1989), it is argued that for vascular epiphytes by far the most relevant abiotic constraint for growth and vegetative functioning is water availability. Other factors, such as nutrients availability or irradiance are generally of less importance (Zotz & Hiertz, 2001, Laube & Zotz 2003). Hemiepiphytes adapt to these constraints through the development of adventitious roots descending to the ground, establishing contact with the soil and transporting water and nutrients (Schimper 1884). These root connections prevent water and nutrient shortage in hemiepiphytes, which is commonplace among holoepiphytes (Williams-Linera & Lawton 1995). However, the aerial roots impose a limit on the height at which a primary hemiepiphyte can become successfully established within tree crowns (Meyer & Zotz 2004). Hemiepiphytes have developed several other morphological and anatomical adaptations to life in the canopy: a lianescent habit (Gill and Tomlinson, 1975), deciduousness (Croat, 1988), leaf paraheliotropism (movement of leaves to avoid or to minimize exposure to sunlight, Mantovani, 2000), leaf succulence and sclerophylly (thickened or hardened foliage that resists loss of moisture), and stomatal and epidermal resistance to water loss (Mantovani, 1999). Their life cycle may imply a size-dependent pattern in light conditions, water-relations and risks that is very distinct from that of trees, lianas or true epiphytes.

Climbing species can be expected to reach higher rates of extension growth (Bøgh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, Schnitzer 2005) than self-supporting species, as their stems have only a limited support function and biomass allocated to them can be invested in stem extension, rather than in rigidity and strength (Bell et al. 1988; Darwin 1867; Putz 1984, den Dubbelden & Verburg 1996). Therefore, it can be expected that secondary hemiepiphytes grow faster in height than self-supported shade-tolerant species (trees), since they make use of the surrounding vegetation to ascend. Secondly, secondary hemiepiphytes have absorbing roots which allow them to be connected to the soil and uptake water and nutrients continuously (Croat 1981) Third, as the plants ascend to the canopy, they will have greater access to light and more absorbing roots, so they can photosynthesize more and obtain more water and nutrients. As a consequence, growth rates are expected to increase with height on the host. However this hypothesis strongly contrasts the findings of Hoffman (1997), who reported a height growth rate of just 0.114 m during six months, with almost half of the plants not growing at all. So far, the size-dependent patterns of growth, survival and reproduction in secondary hemiepiphytes populations have hardly been investigated.

HOST CHARACTERISTICS AND SUITABILITY

As secondary hemiepiphytes, vines and lianas lack the capacity to hold themselves upright, they need to: (1) encounter a suitable host on which to climb; (2) ascend efficiently; and (3) survive the inevitable mechanical demise of their supports (Putz & Holbrook 1991). However, the chance to find a suitable host is maybe low for secondary hemiepiphytes, in similar ways as it is for forest vines (Putz & Holbrook 1991). Therefore, the first need—encountering a suitable support—requires an effective searching strategy, and ideally one that directly results in a host that can sustain the climber throughout its life (Putz 1984). Various hypotheses have been put forward on searching strategies. Strong and Ray (1975) postulated the hypothesis that seedlings of the secondary hemiepiphyte *Monstera gigantea* locate hosts by growing towards the darkness of a tree silhouette, a mechanism that was defined as skototropism (Strong & Ray 1975) or negative phototropism (Kaufman et al. 1989). The searching mechanism of secondary hemiepiphytes has hardly seen any progress since the study of Strong and Ray (1975), although there have been attempts to reveal the relation between *Heteropsis* and other Araceae species and their host (Knap-Vispo et al. 1993, Soares 2008, Lozano-Orihuela & Waechter 2010).

Sexual reproduction starts when individuals have reached a threshold size (Primack & Hall 1990, Mendez & Obeso 1993) that may differ across species of secondary hemiepiphytes. Thus, not all hosts will allow the hemiepiphyte to reach this reproductive size. Therefore, an important characteristic of the host is whether its height is sufficient to allow the secondary hemiepiphytes to reach a reproductive size. If a secondary hemiepiphyte climbs into a non-suitable host, this may entail a “dead-end life history pathway” if it is unable to ‘leave’ that host and search for another host. It has been described that secondary hemiepiphytes produce ramets in the form of flagellar shoots (plagiotropic branches that descent to the ground) that, once they reach the ground, become terrestrial stolons without leaves. Stolons that find a new host generally lose their connection with the ortet (thus becoming a ramet) and often climb up new hosts (Ray 1976, 1992; Andrade & Mayo 1998, 2000, Hoffman 1997). This switch seems to occur when the hemiepiphyte is present on a host that is too short (Ray 1976), if it falls from a tree, or if the tree falls over (Ray 1992). Hemiepiphytes that are able to move to another host (by whatever mechanism) that is sufficiently tall, will grow in size and reproduce, and thereby contribute to the growth of the population. However, depending on the chances to reach a suitable host and the mortality risk of the transition from one to the next host, this contribution to population growth may turn out to be small. So far very little is known about host searching (Strong & Ray 1975), about the fate of plants on non-suitable hosts and about the ways at which secondary hemiepiphytes can escape from non-suitable hosts and their consequences to the population growth.

There has been a strong debate in the literature whether plant species living on hosts (epiphytes, lianas or hemiepiphytes) have certain preferences for host characteristics. While for some epiphytic and liana species host preference has been reported (Migenis & Ackerman 1993, Tremblay et al. 1998, Malizia & Grau 2006, Ladwig & Meiners 2010), Knab-Vispo et al. (2003) found that this was not the case for *Heteropsis* spp. in a tropical lowland rainforest in southern Venezuela. It has been argued that host preference in lianas is related to tree bark characteristics (Talley et al. 1996a) or diameter (Putz 1984, Clark & Clark 1990, Nabe-Nielsen 2001). In contrast, the lack of clearly recognized preferences for lianas might be due to the fact that lianas hanging from a canopy tree may have reached that tree by climbing successive small supports (other trees), leading to incorrect conclusions; or because tree species do not differ in their capacity to act as support structures (Malizia & Grau 2006). That may be the case for secondary hemiepiphytes, which are able to change from host to host during their life (Ray 1976). Consequently, trees seem to be able to carry whatever species of liana or hemiepiphyte that happens to be locally present in the forest.

Secondary Hemiepiphytes In The Genus *Heteropsis* (Araceae)

The genus *Heteropsis* contains about 17 species (Soares et al. 2009) (Table 1), occurring in Central America (Costa Rica and Panama), the Pacific forests of Colombia and Ecuador, and with the greatest number of species in the Amazon region. All species in this genus are secondary hemiepiphytes from primary tropical forests (Croat 1988, Hoffman 1997, Plowden et al. 2003, Balcázar-Vargas & van Andel 2005).

Many studies have been carried out on epiphytic Araceae and a couple of them explored the density and abundance of hemiepiphytic Araceae. Leimbeck & Balslev (2001) studied the abundance and number of epiphytic aroid species in different types of forest in Ecuador, and Knab-Vispo et al. (2003) analyzed the distribution and density of *Heteropsis* spp. in a tropical lowland rainforest in southern Venezuela, and explored the environmental variables that correlate best with the observed *Heteropsis* densities. Hoffman (1997) examined the distribution, harvest response, yield and use of *Heteropsis flexuosa* in several forest sites in Guyana. For Brazilian forests Plowden et al. (2003) described the density of *H. flexuosa* plants and roots; the relationship between *Heteropsis* plants and host tree type and diameter; the maturation time of *Heteropsis* roots; and the impact of simulated harvesting. And finally, there is a synoptical revision of *Heteropsis*, that covers various aspects of their biology, including (micro)-morphology and observations on the ecology and natural history of wild populations in the Reserva Adolpho Ducke, Manaus, Brazil (Soares 2008). As far as we know the demography of hemiepiphytic species has not been analyzed yet.

TABLE 1. Species (Soares 2008 and Soares et al. 2009) and known distributions of *Heteropsis* species (Soares 2008, http://www.tropicos.org, http://sciweb.nybg.org/science2/vii2.asp, http://www.biovirtual.unal.edu.co/ICN/ and personal collections M.P. Balcázar-Vargas).

	Species	Distribution
Heteropsis	*boliviana* Rusby	Bolivia
	croatii M.L. Soares	Brazil (Acre, Amazonas); Peru (Loreto).
	duckeana M.L. Soares	Brazil (Amazonas, Manaus); Colombia (Amazonas).
	ecuadorensis Sodiro	Colombia (Choco); Ecuador (Esmeraldas, Pastaza); Peru (Loreto). Between 50 - 2000 m altitude.
	flexuosa (H.B.K.) G.S. Bunting	Bolivia; Brazil (Amapá, Roraima, Amazonas, Acre, Pará, Maranhão, Rondônia, Pernambuco e Bahia); Colombia (Caquetá, Amazonas, Vaupés, Vichada); Ecuador; Guyana; Peru; Suriname; Venezuela (Amazonas, Atabapo, Apure, Bolivar, Río Negro). Between 50 - 1000 m altitude.
	linearis A.C. Smith	Brazil (Amazonas, Pará, Rondônia); Colombia (Amazonas); Peru (Loreto).
	longispathacea Engl.	Brazil (Amazonas, Acre, Pará, Maranhão); Peru; Suriname.
	macrophylla A.C. Sm	Brazil (Amazonas); Colombia (Caquetá, Amazonas); Ecuador (Napo); Peru (Loreto); Venezuela (Amazonas, Rio Negro, Bolivar).
	oblongifolia Kunth	Bolivia; Brazil (Amapá, Roraima, Amazonas, Acre, Pará, Maranhão, Mato Grosso, Pernambuco, Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, Paraná); Colombia (Caquetá, Amazonas, Choco); Ecuador; Peru (Bagua, Loreto); Venezuela (Bolivar); Costa Rica; Nicaragua. Between 50 - 2000 m altitude.
	peruviana K. Krause	Bolivia; Brazil (Acre, e Rondônia); Peru.
	reticulada Croat & M.L. Soares	Brazil (Acre); Colombia (Amazonas). Around 150 m altitude.
	rigidifolia Engl	Brazil (Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina).
	robusta (G.S. Bunting) M.L. Soares	Brazil (Roraima, Amazonas, Acre, Pará, Mato Grosso); Colombia (Choco, Caquetá, Vaupés); Ecuador (Napo, Pastaza); Peru (Amazonas, Loreto, Iquitos, Pasco); Venezuela (Atabapo, Atures, Bolivar, Río Negro). Between 110 – 1000 m altitude.
	salicifolia Kunth	Brazil (Bahia, Espirito Santo, Minas Gerais, Rio de Janeiro, São Paulo); Colombia; Peru.
	spruceana Schott	Brazil (Roraima, Amazonas, Acre, Pará and Rondônia); Colombia (Caquetá, Amazonas); Guyana; Peru (Loreto); Venezuela (Amazonas, Atabapo, Atures, Bolivar, Río Negro). Between 50-1200 m altitude.
	steyermarkii G.S. Bunting	Brazil (Roraima, Amazonas); Colombia (Amazonas, Caquetá); Ecuador (Pastaza); Guyana; Venezuela (Amazonas, Atabapo, Rio Negro). Between 10-1000 m altitude.
	tenuispadix G.S. Bunting	Bolivia; Brazil (Acre, Amapá, Amazonas, Pará, Rondônia e Roraima); Colombia (Amazonas, Caquetá, Guaviare, Vaupés); Guyana; Peru (Loreto); Venezuela (Atabapo, Atures, Bolivar). Between 30-240 m altitude.
	vasquezii Croat & M.L. Soares	Colombia (Amazonas); Peru (Loreto). Around 150 m altitud.
	melinonii (Engl) A.M.E. Jonker & Jonker	Guiana (species with doubt).

USEFUL ROOTS

Some primary and secondary hemiepiphytes produce strong, pliable aerial roots, used since ancestral times by indigenous people. Nineteen useful secondary hemiepiphyte species are reported for the Amazon (Bennett 1992, Balcázar-Vargas & van Andel 2005). The majority belong to the Araceae (14 species), followed by Cyclanthaceae (5 spp.). The aerial roots are used to make baskets, fish and mammal traps, brooms, and as lashing material for house construction (see Fig. 2 for some examples) (Whitehead & Godoy 1991, Bennett 1992, Paz y Miño et al. 1995, van Andel 2000a, Balcázar-Vargas & van Andel 2005). In the last decades, furniture and handicraft workshops have emerged throughout the Amazon Basin that predominantly use the roots of *Heteropsis flexuosa* (Araceae) as raw material (Hoffman 1997; van Andel 2000a; Wallace & Ferreira 2000; Balcázar-Vargas & van Andel 2005).

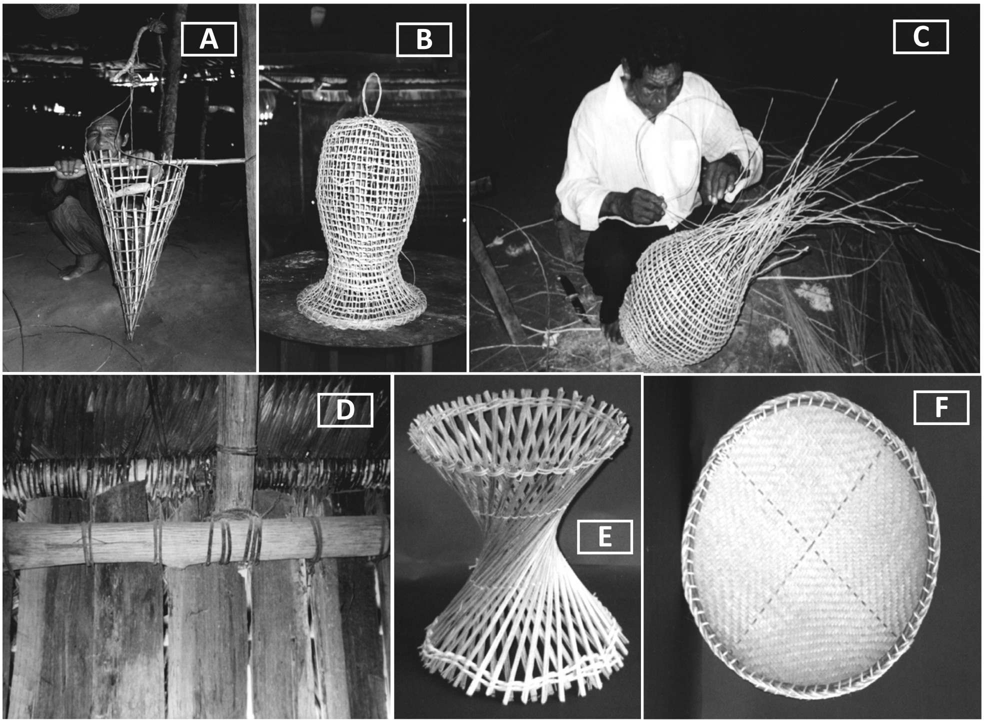


FIGURE 2. **A)** Huitoto fish trap (*te'ki*); **B)** Huitoto fyke or 'female' creel (*rigoru*); **C)** Huitoto creel (*to'naaru*); **D)** Binding material for houses; **E)** Yukuna pot support or magic charm cup (*umichiripuku*) or Piaroa *sämurucä*; **F)** Yukuna balay (*jirú*). (Pictures made by M.P. Balcázar-Vargas, in the Medio Río Caquetá, Amazonas, Colombia).

The most utilized species are *H. flexuosa* (Kunth) Bunting, *H. macrophylla* A.C. Sm, *H. linearis* A.C. Smith, *H. longispathacea* Engl., *H. spruceana* Schott, and *H. oblongifolia* Kunth (Plowden et al. 2003, Balcázar-Vargas & van Andel 2005, Balée, 1994; Paz y Miño et al. 1995;

Troy & Harte, 1998). The vernacular name for Heteropsis most often used in the Brazilian Amazon is ‘‘cipo titica’’, “junco” or “rattan” (Rodrigues, 1989; Troy & Harte, 1998; Wallace & Ferreira, 2000, Callegari-Scipioni et al. 2012). In Colombia, the Spanish term used for the entire genus *Heteropsis* is “yare” in the Caquetá, and “mimbre” in the Brazo Amanaven (Vichada), and the Peruvian term is “tamishi” in the Amacayacu area (Balcázar-Vargas & van Andel 2005, La Rotta et al. 1987), or “tamshi” (Baluarte & del Castillo 2001), and “nibi” in Guyana (Hoffman 1997, van Andel 2000b).

Harvesting Techniques

Harvesting techniques are more or less the same among ethnics groups in the Colombian Amazon (Balcázar & van Andel, 2005). Although some elder women know how to pull down aerial roots, it is almost exclusively a male activity. Either people simply harvest the roots during hunting or fishing activities or, when they need a particular species for production of handicrafts, they organize a collecting trip. Most *Heteropsis* and Cyclanthaceae roots wrap around the trunk of their host trees or contain many knots, making them unsuitable for weaving. The roots preferred for handicraft production are the ones that drop straight from the branches of the tree to the ground. Harvesters look closely at the roots and chose those that are mature (in contact with the soil, absorbing water and nutrients) and have the required pliability, thickness and length. Good quality roots contain few nodes and show no signs of weevil infestation. The desired roots are cut at ground level with a machete, separated from the other entangling roots and carefully pulled down to avoid damage to the ‘mother plant’. Since this is labor-intensive, people occasionally cut down heavily colonized trees in order to obtain the roots (Balcázar & van Andel, 2005).

Can *Heteropsis* Adventitious Roots Be Harvested Sustainably?

The harvest of aerial roots of hemiepiphytes for the production of wicker furniture and basketry has been considered as a promising business in the Amazon Basin (Baluarte & del Castillo 2001, Hall 2000, Hoffman 1997, Plowden et al. 2003, Whitehead & Godoy 1991). First, because *Heteropsis*’ presumed abundance in primary forests has led to optimistic projections about harvest revenues for forest-based communities (Whitehead & Godoy, 1991; Paz y Miño et al. 1995; Troy & Harte, 1998). Second, aerial roots can easily be pulled down and the “mother plant” generally withstands the harvest and stays connected in the canopy and produces new roots (Plowden et al. 2003; Putz & Holbrook 1986). Third, demand for wicker furniture is increasing (Baluarte & del Castillo 2001; Plowden et al. 2003; Whitehead & Godoy 1991). Finally, the roots can be harvested year-round and require extensive manual labor in their conversion into the final product (Balcázar-Vargas & van Andel 2005). When roots are only used for subsistence activities, extractors generally remove only two or three mature roots per plant, even if more suitable roots are present. For commercial handicraft production, much larger quantities are needed and indigenous management systems are quickly abandoned. Hemiepiphytes are becoming scarce around the communities and people have to walk further in the forest in order to collect their fibers. This situation has been described for many places throughout the Amazon, especially in areas where baskets or wicker furniture from the roots are manufactured for the market (Hoffman 1997, Plowden et al. 2003, Balcázar-Vargas & van Andel 2005, Callegari-Scipioni et al. 2012). It has been argued that present harvesting intensities for aerial roots are not sustainable. Harvesting experiments in Guyana (Hoffman 1997) and Brazil (Plowden et al. 2003) showed that harvesting more than 50% of the mature roots had a negative effect on the reproduction and survival of hemiepiphytes. However, the consequences at the population level have never been studied. The extraction of non-timber forest products (NTFP) can only be considered as sustainable when populations do not become extinct as a result of exploitation, and when the productivity of the populations (in terms of availability of the extracted product) does not decline (Zuidema 2000). While overharvesting of NTFPs is often associated with contemporary commercial exploitation (Pedersen & Balslev 1992, Zuidema 2000), indigenous overharvesting of preferred species also occurred before the advent of Western civilization (Davis & Yost 1983, Roth 1924).

Why This Study?

From 1998 to 2001, I studied the ethnobotany of secondary hemiepiphytic species used by seven different ethnic groups from the north to the south of the Colombian Amazon (Balcázar-Vargas & Sastoque 1999, Balcázar-Vargas 2000, Balcázar-Vargas 2002, Balcázar-Vargas & van Andel 2005). Since commercial handicraft production demanded increasingly larger quantities of roots and the indigenous management systems were quickly abandoned, hemiepiphytes were becoming scarce around the communities in the Amanaven area, Colombia (Balcázar-Vargas & van Andel 2005). Based on that study and literature research, I realized that it was necessary to conduct a study on the population dynamics of these species, in particular those of the genus *Heteropsis*, the most important and widely used group for craft fibers. Information on the demography of commercial species and the impact of their exploitation is essential to assess the impact on future resource availability (Hall & Bawa 1993). Only with information about the vital rates, the fate of plants on non-suitable hosts, their consequences to the population growth and their demography and harvesting experiments, sustainable harvest levels could be calculated. With this information, forest people will have the tools to continue the root harvesting to supply their income without depleting the resource.

Study Region

This study was carried out in the Amazonas department, in the Biological station El Zafire (BSZ) located at (4º0’20.9’’S and 69º53’55.2’’W) in the Trapecio, in the Colombian Amazon (Fig. 3). The climate in the region is characterized by an average annual rainfall of 3335 mm (data from the Vásquez Cobo airport of Leticia, Jimenez et al. 2009), a mean annual temperature of ca. 26 °C and a relative humidity of 86 % (Jiménez 2007). Altitude is about 80 m above sea level. The vegetation is composed of species-rich humid tropical forest, with white-sand forest, floodplain forest and tierra firme forests (Peñuela & Alvarez, 2006). Various indigenous tribes inhabit the region: Tikuna, Huitoto, Bora, and some isolated members of the other indigenes groups (DNP 2002). Population density in this region is less than 0.04 people per km². More than 75% of the Amazon Department area has been declared as Amerindian resguardos, which gives the indigenous inhabitants collective ownership of this territory (van der Hammen 2003). The environmental policy of the Colombian government for the Amazon Basin tries to combine conservation with development, looking for improvement of living conditions for the human population within an ecologically viable framework (DNP 1991).

In the area around the Biological station El Zafire, 10 species of *Heteropsis* can be found: *H. duckeana, H. ecuadorensis, H. flexuosa, H. linearis, H. macrophylla, H. oblongifolia, H. reticulada, H. rigidifolia, H. steyermarkii,* and *H. tenuispadix.* Botanical collections on these species were deposited at the Herbario Nacional Colombiano (COL) under Maria Paula Balcazar's collector name (MPB; see Appendix 1). During this PhD project, I studied three sympatric *Heteropsis* species in the Colombian rain forest: *H. flexuosa* (Kunth) G.S. Bunting, *H. macrophylla* A.C. Sm and *H. oblongifolia* Kunth. This species selection was based on abundance and economic importance.

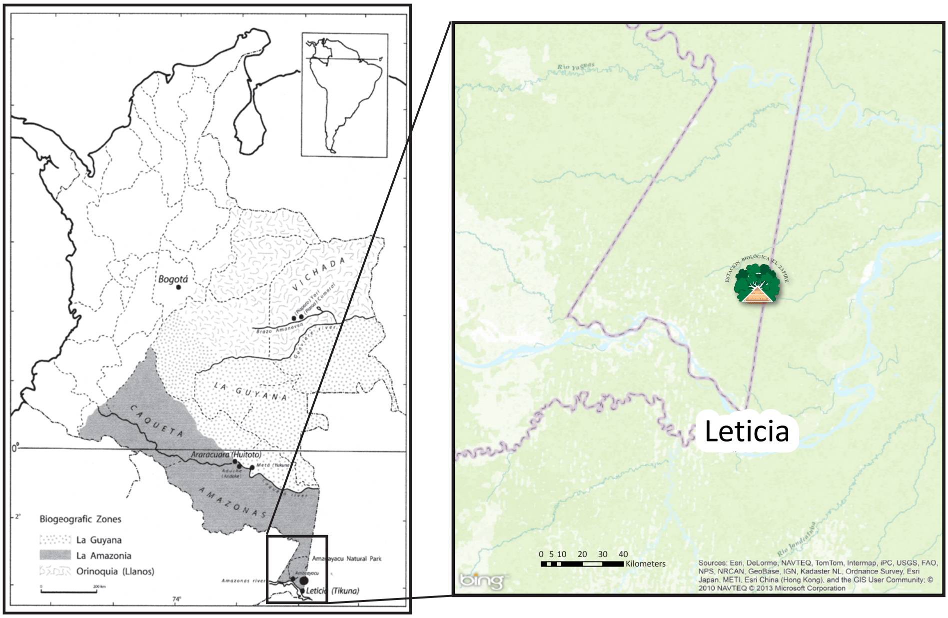


FIGURE 3. Location of the research area •. El Zafire Biological research station (ZBS). (Left map by Hendrik Rypkema, National Herbarium of the Netherlands. Right SIG map by Thijs de Boer).

OBJECTIVES OF THIS STUDY

This PhD study aimed to improve our understanding of the life history, population dynamics and host searching strategy of three sympatric *Heteropsis* species (secondary hemiepiphytes) in the Colombian Amazon. The objectives of the present study were:

1.To provide insight into how three sympatric *Heteropsis* species search for a host.

2. To describe and explain patterns of survival, growth, retrogression, vegetative and sexual reproduction of the three *Heteropsis* species and the implications of the host suitability for these vital rates.

3. To provide insights into the main drivers of population growth of the three *Heteropsis* species, with particular focus on the contribution of subpopulations on suitable and non-suitable hosts to population growth and the importance of vegetative reproduction to population growth.

4. To estimate the age at which *Heteropsis* species become reproductive and at which their roots can be harvested.

OUTLINE OF THIS THESIS

This thesis addresses the demography and the relative importance of host suitability of three species of *Heteropsis* used for the manufacture of indigenous basketry and handicrafts across the Amazon.

Chapter 2 describes the host-searching strategies of the three *Heteropsis* species, using information on the size distribution of hosts with climbing *Heteropsis* individuals and the suitability of those hosts. We analyze this for seedlings of the three *Heteropsis* species as well as for vegetatively produced ramets.

Chapter 3 discusses the results of a study on survival, growth, reproduction and vegetative propagation of the three *Heteropsis* species and the implications of host suitability for these vital rates. With these data we quantify and evaluate the effect of plant height, plant size and host suitability on these vital rates. The importance and consequences of vegetative propagation are further discussed.

Chapter 4 analyses the demography of three *Heteropsis* species, using multi-state population models. In this chapter I separated dynamics of *Heteropsis* on suitable vs. non-suitable hosts in order to determine the relative contribution of plants on non-suitable hosts for population growth. I also quantified the importance of vital rates, particularly focusing on the importance of the forms of vegetative reproduction that allow *Heteropsis* plants to change hosts and survive after host mortality.

Drawing of *Heteropsis flexuosa* showing an inflorescence (Drawing by Maria Teresa Vargas-Paz).

Chapter 2

The Quest for a Suitable Host: Size Distributions of Host Trees Suggest that Secondary Hemiepiphytes Adopt a Random Searching Strategy

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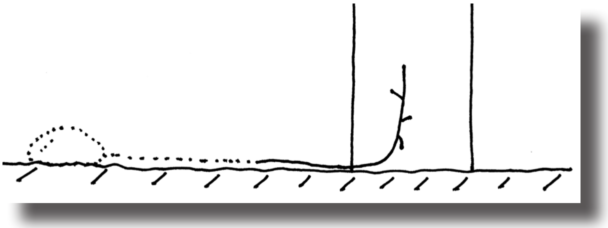
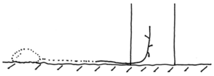




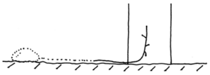
The Quest for a Suitable Host: Size Distributions of Host Trees Suggest that Secondary Hemiepiphytes Adopt a Random Searching Strategy

ABSTRACT

As climbing plants lack the capacity to hold themselves upright, they need to encounter a suitable host. Vines, lianas, and secondary hemiepiphytes need therefore an effective searching strategy. Various hypotheses have been put forward on searching strategies, including 'skototropism' – growth towards darkness – and random searching. We studied host searching strategies of three secondary hemiepiphyte species belonging to the genus *Heteropsis*. We recorded information on the diameter distribution of host and evaluated whether these hosts were 'suitable', i.e. sufficiently tall for *Heteropsis* individuals to reach reproductive size. The diameter distribution of host trees bearing *Heteropsis* seedlings was similar to that of the trees in our study plots. Also, we found that 72-81 percent of the *Heteropsis* seedlings were present on unsuitable hosts (seedlings, saplings, herbs). These results suggest that *Heteropsis* seedlings search hosts in a random manner and not by skototropism. We found quite a distinct pattern for adult *Heteropsis* individuals, which predominantly occur on host trees bigger than 10 cm DBH. Host diameter distribution for *Heteropsis* adults differed significantly from that of the entire tree community. This difference suggests that *Heteropsis* individuals may change hosts if they are initially present on non-suitable hosts. We observed that *Heteropsis* seedlings and juveniles on unsuitable hosts often produced vegetative shoots that searched for another host. In many cases, such shoots did not find a suitable host. For *Heteropsis*, our results suggest that host tree searching is a long-term trial and error process which is governed by a random searching strategy.

RESUMEN

Debido a que las plantas trepadoras carecen de la capacidad de sostenerse en una posición vertical, es necesario que estas encuentren un hospedero adecuado. Por lo tanto enredaderas, lianas y hemiepífitas secundarias requieren de una estrategia efectiva para la búsqueda de un hospedero. Se han propuesto varias hipótesis en las estrategias de búsqueda, incluyendo el skototropismo (crecimiento hacia la oscuridad) y la búsqueda al azar. Se estudiaron las estrategias de búsqueda de tres especies de hemiepífitas secundarias pertenecientes al género *Heteropsis*. Se registró la información de la distribución del diámetro de los hospederos y se evaluó si estos eran "adecuados", es decir, si eran lo



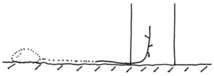
suficientemente altos para que los individuos de *Heteropsis* pudieran alcanzar el tamaño reproductivo. La distribución del diámetro de los árboles hospederos en los cuales estaban trepadas las plántulas de *Heteropsis* fue similar a la distribución de todos los árboles en nuestras parcelas. Además, se encontró que del 72 al 81 por ciento de las plántulas de *Heteropsis* estaban trepadas en hospederos inadecuados (plántulas, hierbas). Estos resultados sugieren que las plántulas de *Heteropsis* buscan los hospederos de una forma aleatoria y no por skototropismo. Se encontró un patrón muy distinto para los individuos adultos de *Heteropsis*, los cuales ocurren predominantemente en árboles mayores de 10 cm de DAP. La distribución del diámetro de los hospederos de *Heteropsis* adultos difirió significativamente de la comunidad entera de árboles. Esta diferencia sugiere, que los individuos de *Heteropsis* pudieron cambiar de hospedero cuando ellos estaban inicialmente presentes en un hospedero no adecuado. Se observó que las plántulas y los juveniles de *Heteropsis* que están en hospederos no apropiados, a menudo producen brotes vegetativos que buscan nuevos hospederos. En muchos casos, estos brotes no encontraron un hospedero adecuado. Nuestros resultados sugieren que la búsqueda de hospederos en *Heteropsis*, es un proceso de ensayo y error que se rige por una estrategia de búsqueda aleatoria.

Key words: *Araceae, Colombia; Heteropsis; host trees; secondary hemiepiphytes; skototropism; tropical forest.*

INTRODUCTION

Climbing plants such as vines, lianas and secondary hemiepiphytes are typical and important components of tropical forests and can represent up to 20 – 25 percent of the vascular flora (Gentry & Dodson 1987, Croat 1988, Gentry 1991, Gentry 1992, Nabe-Nielsen 2001, Schnitzer & Bongers 2002). The overall species diversity of climbing plants in the tropics is high, with over 8000 species of vines and lianas (Gentry 1991), and about 700-1000 species of secondary hemiepiphytes (Croat 1988, Williams-Linera & Lawton 1995). Many of these species lack the capacity to hold themselves upright, thus these climbing plants need to (1) encounter suitable structures on which to climb, (2) ascend efficiently, and, (3) survive the inevitable mechanical demise of their supports (Putz & Holbrook 1991). The first need – encountering a suitable support – requires an effective searching strategy, and ideally one that directly results in a host tree that can sustain the climber throughout its life (Putz 1984).

One of the most intriguing questions in climbing plant ecology is how vines, lianas and secondary hemiepiphytes find a suitable host (Strong & Ray 1975). Strong and Ray (1975) showed in an experimental study that seedlings of the secondary hemiepiphyte, *Monstera gigantea*, find hosts by growing towards the darkness of a tree silhouette, a mechanism that was termed skototropism (Strong & Ray 1975) or negative phototropism (Kaufman et al. 1989).



In spite of the interest in host searching by secondary hemiepiphytes, this topic has hardly been studied so far. We studied the host searching behavior in *Heteropsis*, a genus consisting of secondary hemiepiphytes found in primary tropical moist forests (Croat 1988, Hoffman 1997, Balcázar-Vargas & van Andel 2005). After germinating on the forest floor, *Heteropsis* seedlings produce a leafless stem that moves away from the germination spot (Fig. 1). When this stem finds a host, it climbs up using adventitious anchoring roots (Wilder 1992, Romero 1994). Once the plant is attached, absorbing roots are formed growing downwards. When these roots reach the soil, the lower part of the stem dies. The plant continues to grow up, producing plagiotropic branches and more absorbing roots, and gradually shedding its lower parts (Putz & Holbrook 1986, Plowden et al. 2003). *Heteropsis* species reproduce sexually, but also form ramets that can then climb up in other host trees.

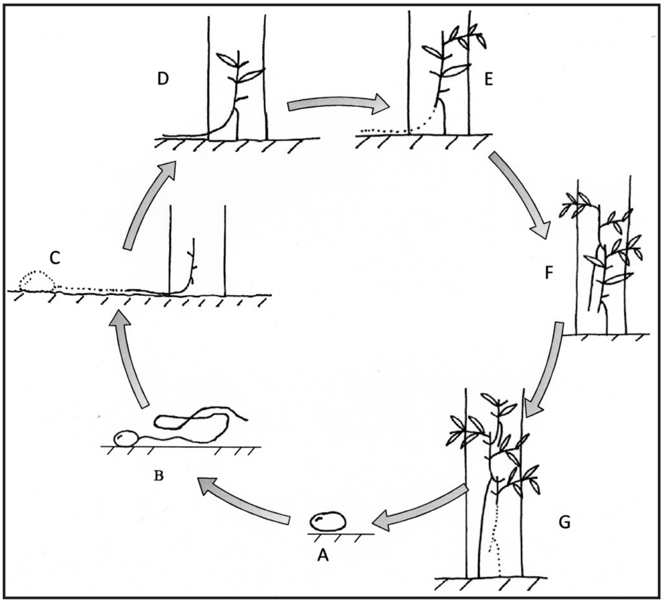
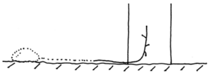


FIGURE 1. The life cycle of *Heteropsis* species. **A)** Seed on the forest floor. **B)** Seed germinates. **C)** Seedling finds a host and adheres to it. **D)** An absorbing root sprouts and grows downward until it reaches the soil. **E)** The stem loses connection to the soil. **F)** and **G)** The hemiepiphyte grows and becomes reproductive. The lower stem senesces together with the lowest root(s). Drawing by M.P. Balcázar-Vargas.

We studied three sympatric *Heteropsis* species in a Colombian rainforest. We collected information on diameter distributions of *Heteropsis* hosts and about the diameter distribution of all trees in our study plots. We also assessed whether these hosts are suitable in the sense that they are sufficiently tall to allow *Heteropsis* individuals to reach reproductive size. Finally, we determined whether *Heteropsis* individuals that change host by clonal propagation find a more suitable host, or not. We addressed the following questions: (1) Do hosts of *Heteropsis* seedlings differ in size (diameter) from those of *Heteropsis* adults?



(2) Is the size distribution of *Heteropsis* hosts similar to the distribution of tree sizes in the entire tree community? Answering the latter question provides insight into the mechanisms of host tree searching: if seedlings search hosts in a random fashion, such similarity would be expected, but if they do so by skototropism, one would expect them to be present on the largest trees in the forest (in terms of diameter). (3) What proportion of hosts of *Heteropsis* individuals are suitable? And (4) what is the chance that a *Heteropsis* individual present on a non-suitable host finds a suitable host through production of vegetative shoots? Finally, we also evaluated whether host searching behaviour differed across our three study species.

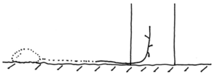
METHODS

STUDY SPECIES

The genus *Heteropsis* contains about 17 species (Soares et al. 2009), distributed in Central America (Costa Rica and Panama), the Pacific forest of Colombia and Ecuador, and has the largest number of species in the Amazon region (Croat 1988, Plowden et al. 2003). We studied *H. flexuosa* (Kunth) G.S. Bunting, *H. macrophylla* A.C. Sm and *H. oblongifolia* Kunth. These species differ in the maximum height that they reach in host trees. In our study plots, the maximum observed height on a host was 14 m for *Heteropsis oblongifolia*, 25 m for *H. flexuosa* and 35 m for *H. macrophylla*. The species also differ in the height on the host tree at which they become reproductive. To determine the minimum required height of a host trees to allow individuals of these species to become reproductive, we have recorded the reproductive status for 132, 93 and 109 individuals of *H. flexuosa*, *macrophylla* and *oblongifolia*, respectively, every month, during two years. For each of these individuals we also recorded their upper height on the host. We recorded the inflorescence production of *H. flexuosa* from 7 m; *H. macrophylla* from 8 and *Heteropsis oblongifolia* from 1 m on a host tree. For the 51, 58, and 16 reproductive individuals that we observed, we found that the 99 percent of *H. flexuosa* and 100 percent of *macrophylla* produced inflorescences at heights of ≥ 10 m and 100 percent of *H. oblongifolia* at heights of ≥ 1.5 m.

STUDY SITE

Field work was conducted at El Zafire Biological research station (ZBS) of the Universidad Nacional de Colombia from February to September 2007, and the same period in 2008 and 2009. ZBS is located in the southern-most part of the Colombian Amazon at 4°0’ S, 69°53’ W with an elevation of approximately 80 m asl (Fig. 3 in Chapter 1). The mean annual temperature is 26 °C with a relative humidity of 86 percent (Jiménez 2007). This area has sandy soils and four major types of forest (tierra firme, floodplain, white sand and transition forest). These are all old-growth forests, with no evidence of human disturbance except for hunting.



SAMPLE DESIGN AND FIELD MEASUREMENTS

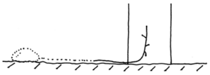
We conducted the study in three plots in undisturbed tierra firme forest; two of which are permanent plots included in the RAINFOR network (Peñuela & Alvarez 2006). The three plots measured 0.7, 1 and 4 ha. To evaluate the diameter distribution of the entire tree community, we measured the diameter at breast height (DBH) for all trees, lianas and palms ≥10 cm DBH in these three plots (N= 3600, measured in 2007).

We categorized hemiepiphyte individuals into three life cycle stages: seedlings (P), juveniles (J) and adults (A), based on the upper height on the host and the minimum height at which the plant becomes reproductive. *Heteropsis flexuosa* and *H. macrophylla* were considered to be seedlings if they were searching for a host (Fig. 1B) or climbing a host to ≤1 m height (Fig. 1C-E). Juveniles were defined as having an upper height of 1-10 m and adults ≥10 m. In *H. oblongifolia*, seedlings were <50 cm tall; juveniles had an upper height of 0.5-1.5 m, and adults ≥1.5 m, which is the height of onset of reproduction. Finally recruited seedlings (R) were the new seedlings found in 2008 and 2009.

In 2007, we searched, tagged and measured adults, juveniles and seedlings of the three *Heteropsis* species in the three plots, following standard practice for nested plot design (Elzinga et al. 2001). Adult individuals were searched in the entire plot, juveniles in 49 subplots of 20 x 20 m, (1.96 ha), and seedlings in 49 subplots of 10 x 10 m (0.49 ha). All subplots were randomly chosen within the plots, until we found about 250 – 300 seedlings and 150 - 200 juveniles. In 2008 and 2009 the recruited seedlings (R) of the three species were searched, tagged and measured in the seedlings subplots (0.49 ha). We included these recently recruited seedlings because we were interested in the characteristics of the first host on which these seedlings climb.

For each *Heteropsis* individual, we measured its upper and lower height on the host tree, employing a fiberglass telescopic rod or a measuring tape using climbing techniques. Furthermore, we recorded whether individuals had a branch that climbed up another host. If during the next census we would find that this branch had lost connection with the parent plant ('ortet') we recorded this 'ramet' as a new individual, produced by clonal propagation. We recorded the production of ramets in 2008 and 2009. To facilitate the interpretation of branching and ramet production, we made drawings of all measured individuals every year.

For each *Heteropsis* host, the following variables were recorded: (1) diameter at breast height (DBH) (for hosts with a height lower than 1.3 m, the stem diameter was recorded at half the trunk height), (2) total height and height of first branch, (3) whether the host was dead or alive, upright or fallen down, and its inclination. Then we categorized a host as 'non-suitable' or 'suitable', based on the minimum height at which the three *Heteropsis* species reproduce, the host's inclination and whether it was alive or dead (e.g., of non-suitable host were small palms like *Lepidocaryum tenue* Mart.; herbs like Marantaceae



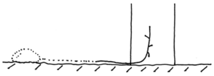
and Heliconiaceae; tree seedlings, tree ferns, and dead plants). We did not specifically record information on bark characteristics of host trees, but we did not find any *Heteropsis* individual on a tree with peeling bark, and just one on a tree species which loses its bark as dust. In this particular case, we classified this host as non-suitable. A suitable host tree for *H. oblongifolia* needed to be alive, taller than 1.5 m and with an inclination less than 45 degrees. The criteria of suitability were the same for *H. flexuosa* and *H. macrophylla*, but with a minimum height of 10 m. In addition, we created a category called "probably suitable", which we included the hosts that were not sufficiently tall for an *Heteropsis* plant to become reproductive at the moment of the research, but were judged to become suitable after some years, based on information of typical tree height growth rates (Rozendaal 2010). Using this information, we assumed that it would take 12-25 years for a tree of 6 m tall to reach 10 m. Thus, 'probably suitable' hosts were defined as saplings of 1-1.4 m tall for *H. oblongifolia*, and saplings of 6-9 m tall for *Heteropsis flexuosa* and *macrophylla*. In total, we measured 792 individuals of *Heteropsis flexuosa* (*Hf*), 690 of *H. macrophylla* (*Hm*) and 655 of *H. oblongifolia* (*Ho*).

In order to increase sample size on initial host tree searching behavior (Category B in Fig. 1), we selected 10 fertile individuals per species outside the permanent plots and established 10 x 10 m plots around each of these. In April 2008, September 2008, and September 2009 we searched recruited seedlings of the species in each plot (N=30 plots). The seedlings searched and observed in these plots were not used for the statistical analysis, because they were not randomly chosen. We use this data only to describe initial host searching behaviour. In these plots we measured 151 seedlings of *Heteropsis flexuosa* (*Hf*), 163 of *H. macrophylla* (*Hm*) and 47 of *H. oblongifolia* (*Ho*).

STATISTICAL ANALYSIS

We established the size distributions of host based on the DBH of the host. We did so for various size categories of the *Heteropsis* species: seedlings, juveniles and adults. We compared the host size distributions among *Heteropsis* categories using a Chi-square test (for *H. flexuosa* and *H. macrophylla*) and a Fisher's exact Chi square test (for *H. oblongifolia*), because some cells had expected counts of <5. Across species, we also tested for differences in host size distribution, using-Fisher's exact Chi square test for the seedlings (because some cells had expected counts of <5) and a normal Chi-square test for juveniles and adults. In case of significant differences between the species, we tested which species causes the difference employing the Pairwise Comparisons with a Bonferroni corrected *P*-value.

We also tested for differences between the diameter distributions of *Heteropsis* host and the diameter distributions of the entire tree community (all trees, palms and lianas in the forest ≥10 cm DBH, N=3600). We compared these distributions for each of the three *Heteropsis* categories: seedlings, juveniles and adults, using a Chi-square goodness of fit test. Thus, in this case only those *Heteropsis* individuals that were present on trees, lianas and palms ≥10 cm DBH were included, and not those climbing in tree seedlings or saplings.



As for the suitability of host, we compared the distribution of *Heteropsis* individuals over host suitability classes (non-suitable, probably suitable and suitable) across *Heteropsis* size categories within a species. We also performed similar tests to uncover differences across species in this distribution, again using a Chi-square test, per *Heteropsis* size category. In case cells had expected counts of <5, we applied Fisher's exact test. In case of significant differences, we applied the Pairwise Comparisons using Bonferroni corrected *P*-values.

We were also interested in finding out whether the new ramets produced by an ortet find a suitable host. To this end, we compared the host suitability of the ortet before the ramet production with the host suitability of the new ramet(s). We also compared the host suitability of the ortet but only with the ramet that climbed the best host. We applied Chi-square goodness of fit tests for both analyses. All statistical analyses were conducted using the software SPSS 16 (SPSS Inc., U.S.A.).

Results

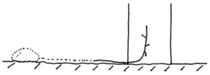
Observations On Initial Host Tree Searching Behavior

Stems of leafless *Heteropsis* seedlings grew on the forest floor over a distance of half a meter (Average= 0.45 m; SD=0.31 m; N=19). Of the 71 (*Hm*:45, *Hf*:24 and *Ho*:2) newly recruited seedlings (Fig. 1 B, C, D and E) that we encountered for all three study species, 91 percent had found a host within six months. Based on the seedling recruitment data by 10 x 10 plots and in the three permanent plots we observed that survival of non-climbing seedlings was very low, just 28 percent annually (N=39; *Hm*:17 and *Hf*:22; Fig. 1B).

Host Size Distributions Of *Heteropsis* Seedlings, Juveniles And Adults

Established, climbing seedlings of all three *Heteropsis* species were mostly found on small hosts. The smallest diameter category of hosts (0.1-2.49 cm DBH) contained the majority of the *Heteropsis* seedlings (54-65%). Overall, the size distribution of host trees of *Heteropsis* seedlings had an inverse J-shape (Fig. 2).

In contrast to *Heteropsis* seedlings, adults of *H. flexuosa* and *H. macrophylla* were found predominantly on large trees. For instance, 95-96 percent of the *Heteropsis* adults climbed hosts ≥10 cm DBH (Fig. 2). In contrast, 73 percent of the adults of *H. oblongifolia* were found on the smallest hosts (0.1-9.9 cm DBH). The differences in host size distributions across *Heteropsis* seedlings, juveniles and adults were highly significant for all three species (Pearson Chi-square: *Hf*: $\chi2$=2.185E2, *P*=0.000 *df*:12 and *Hm*: $\chi2$=2.067E2, *P*= 0.000, *df*:12; Fisher's exact Chi square test *Ho*: $\chi2$=40.045, *P*=0.000). Thus, hosts of *Heteropsis* seedlings differed in size from those of *Heteropsis* adults.



Comparing across *Heteropsis* species, the host size distributions of *Heteropsis* adults differed between species (Chi-square $\chi2$=1.645E2, *P*=0.000, *df*:12). Host size distributions of *H. flexuosa* and *H. macrophylla* did not differ (Pairwise Comparisons using Bonferroni corrected *P*-value: adults: $\chi2$=6.749, *P*=0.981). Yet the distribution of *H. oblongifolia* did differ, having almost 91 percent of the juveniles' individuals climbing up in the two smallest DBH categories (Fig. 2).

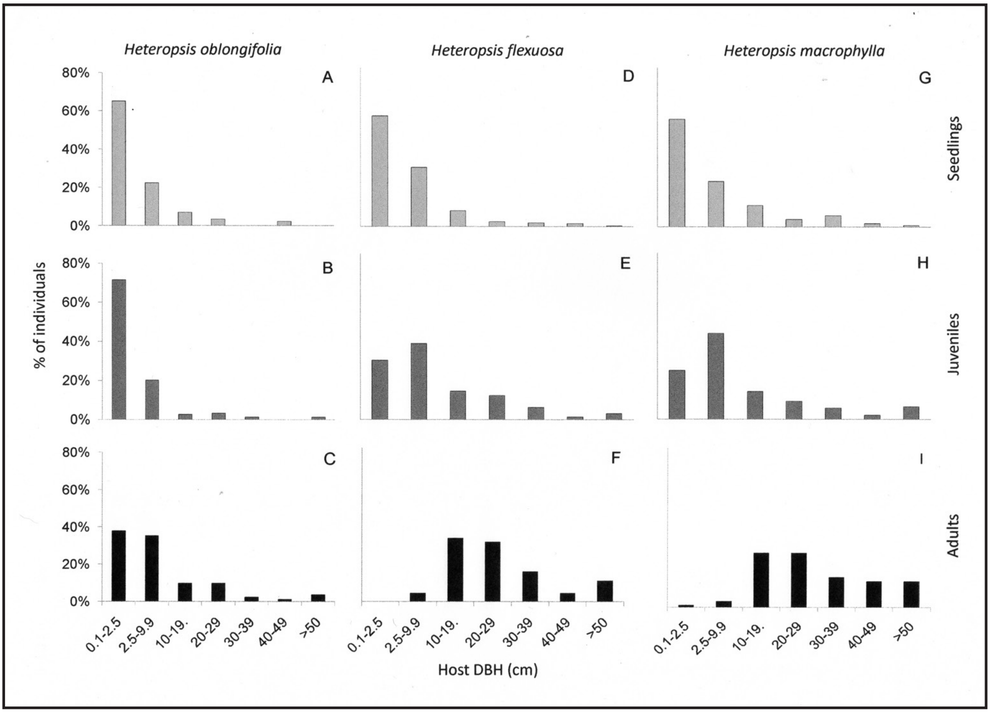


Figure 2. Host size distributions for seedlings (**A, D, G**), juveniles (**B, E, H**) and adults (**C, F, I**) of three *Heteropsis* species. Showing the standard error of the three plots. See text for results of statistical tests.

COMPARING SIZE DISTRIBUTIONS OF HOSTS WITH THAT OF THE ENTIRE COMMUNITY

The diameter distribution of hosts of *Heteropsis* seedlings was very similar to that of all trees, palms and lianas of ≥ 10 cm DBH in the plots. Thus, here we consider only those *Heteropsis* individuals that are present on trees (or palms and lianas) ≥10 cm DBH, and compare the size distribution of these hosts with that of the entire tree population. In both cases, the diameter distributions showed clear inverse J-shapes (see Fig. 3). Chi-square tests indeed revealed no differences between these distributions for seedlings of *H. flexuosa* and *H. macrophylla* (Chi square goodness of test: *Hf*: $\chi 2$=4.11, *P*=0.391, *df*:4, and *Hm*: $\chi 2$=8.64, *P*=0.0708, *df*:4). By contrast, the diameter distribution of *Heteropsis oblongifolia* seedlings differed significantly from that of all trees in the plots (Chi square goodness of test: $\chi 2$=14.73, *P*=0.0053, *df*:4).

When considering the diameter distributions of host for *Heteropsis* juveniles and adults we found that these distributions differed significantly from that of all trees, palms and lianas ≥ 10 cm DBH in the plots (Fig. 3; Chi-square goodness of fit: *Ho* juveniles: $\chi 2$=10.41, *P*=0.0341, *df*:4, adults: $\chi 2$=16.32, *P*=0.0026, *df*:4. *Hf* juveniles: $\chi 2$=12.14, *P*=0.0163, *df*:4, adults: $\chi 2$=50.70, *P*=0.0000, *df*:4. *Hm* adults: $\chi 2$=70.33, *P*=0.0000, *df*:4). This was consistently found for all *Heteropsis* species. *Heteropsis* occurred on a significantly lower percentage of hosts between 10-19 cm DBH and on a significantly higher percentage of trees, palms and lianas with DBH ≥20 cm than expected, in all size classes and species. Moreover, the percentage of seedlings present on host of 10-19 cm DBH is greater than the percentage of juveniles and adults in the same DBH category; decreasing gradually the percentage from seedlings to adults. By contrast, the percentage of seedlings present in trees, palms and lianas ≥20 cm DBH is lower than the percentage of juveniles and adults in the same categories. These results are consistent for the three species

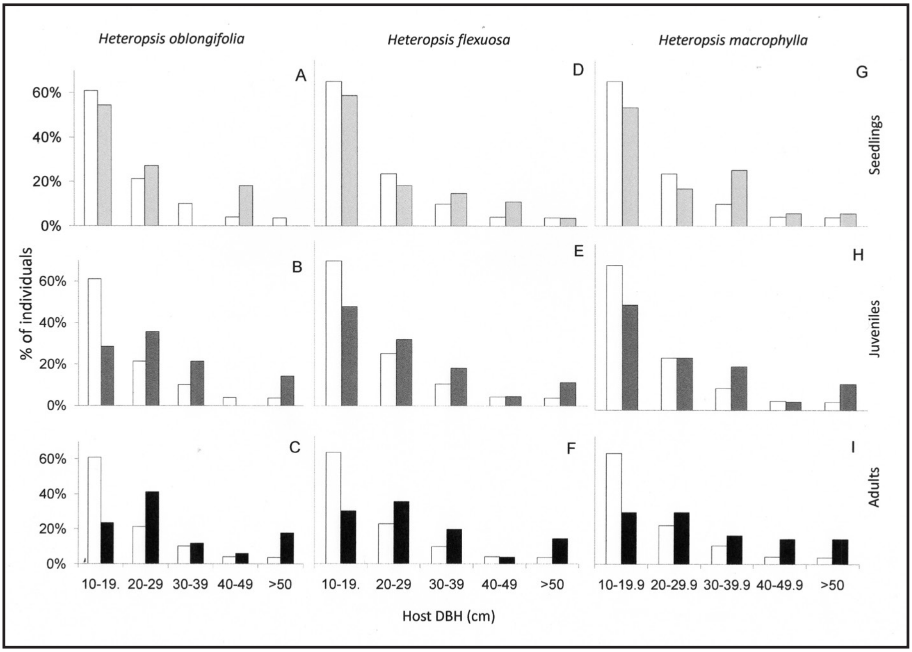
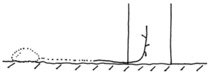


FIGURE 3. Comparing the size distributions of trees in the three plots (DBH ≥10 cm, n=3600) (white bars) vs. host size distributions of three *Heteropsis* species. Comparisons are made for *Heteropsis* seedlings (light grey bars, **A, D, G**), juveniles (dark grey bars, **B, E, H**) and adults (black bars, **C, F, I**).



HOST SUITABILITY

The majority (72 to 81%) of recruited seedlings (R) of all three study species that had recently climbed their host were growing on small, non-suitable, hosts. In many cases, these hosts included herbs (2.1%), tree seedlings (6.5%), understory palms (10.2%) and dead plants (6.2%). The same was found for established seedlings (P) for two of the study species: *H. macrophylla* (69%) and *H. flexuosa* (72%). For *H. oblongifolia* a significantly higher proportion of established seedlings climbed up a suitable host (50%; Chi-square: $\chi2=70.015$, $P= 0.000$, $df= 4$). We also found significant differences in the percentages of suitable hosts among juveniles (J) of the three species (Chi-square: $\chi2=46.026$, $P= 0.000$, $df= 4$). *H. oblongifolia* had the highest percentage of suitable hosts in this category (72%) (Pairwise comparisons corrected using Bonferroni: $\chi2=34.682$, $P= 0.000$, $df= 2$). We did not find significant differences between adults (A) of the three species in the percentage of non-suitable, probably suitable and suitable hosts (Fisher's Exact test: $\chi2=1.617$, $P=0.851$). The proportion of suitable hosts increased from the category of recruited seedlings, to adults for all three species, with the latter having the largest proportion of suitable hosts (94 – 97%) (Fig. 4). For the three species there was a significant difference in the proportion of individuals on the three types of hosts (suitable, probably-suitable and non-suitable) per category (Chi-square: *Ho*: $\chi2=89.896$, $P=0.000$, $df= 6$; *Hf*: $\chi2=2.026E2$, $P=0.000$, $df= 6$; *Hm*: $\chi2=1.789E2$, $P=0.000$, $df= 6$.).

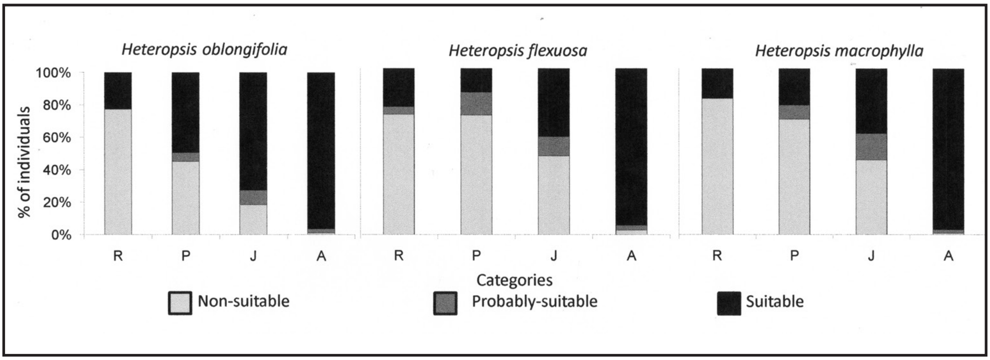
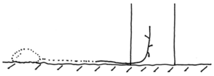


FIGURE 4. Host-tree suitability for three species of *Heteropsis*: Shown are the percentages of *Heteropsis* individuals on three types of host (non-suitable, probably suitable and suitable), for each of four size categories: recruited seedlings (R), established seedlings (P), juveniles (J) and adults (A). See text for results of statistical tests.

PRODUCTION OF RAMETS

Between 4.3 and 4.7 percent of the individuals on hosts of the three species produced ramets from 2007 to 2009 (Table 1). Five types of clonal propagation were observed, many of which results in a change of host (Fig. 5, B, C, D and E). We observed that *Heteropsis*



individuals on non-suitable hosts, very often were producing flagellar shoots to the ground. Shoot production started at an average 60 cm (N=27, SD= 0.242) below the top of that non-suitable host. Flagellar shoots that found new hosts generally lost the connection with the ortet, after one or two years, thus becoming an independent ramet (Fig. 5, B). We occasionally found plagiotropic branches touching a nearby tree; some of these branches developed a shoot that climbed the nearby host, loosing contact with its mother plant and thus can be treated as a ramet (Fig. 3, E). Other type of clonal propagation occurs if the plant falls (with or without host) and survives (15.3 - 46.6%), then the plagiotropic branch produces stolons that climb up new hosts, and eventually separate (Table 1; Fig. 5, C).

TABLE 1. Percentage of the individuals per type of cloning in the three *Heteropsis* species. The letters A to E refers to the type of cloning of the Figure 5.

Species	Percentage of occurrence of cloning type (%) per year					
	A	**B**	**C**	**D**	**E**	**Total (not include C)**
Heteropsis oblongifolia	1.45	2.42	46.58	0.10	0.29	4.26
Heteropsis flexuosa	3.02	0.85	19.81	0.30	0.20	4.37
Heteropsis macrophylla	3.42	0.55	15.33	0.46	0.28	4.71

A to E: referring to the type of cloning in the Figure 5.

CHANGING HOSTS TO FIND A SUITABLE ONE

Between 2007 and 2009 we observed a small fraction (1.3 to 2.8 %) of *Heteropsis* individuals on hosts changing host (Fig 5, B, D, E; Table 1, B, D, E). Of the three species, *H. oblongifolia* fallen plants exhibited the highest frequency of producing ramets (Fig 5, C; Table 1, C); and even though a relatively high proportion of individuals belonging to this species were already located on a suitable host, they produce a higher proportion of ramets (Table 1, B; Fig. 4). Seedlings and juveniles changed hosts more often than adults: between 1.9 and 5.9 percent of seedling changed host or sent shoots searching for a new stem to ascend, while this was just 1.0 and 3.1 percent for adults.

Changing hosts by clonal propagation was found rather frequently: every year 0.8 - 2.7 percent of the genetic individuals – ortets – sent out branches – ramets – that were searching for new hosts (Fig 5, B, E; Table 1, B, E). A comparison of the suitability of hosts ortet and the host of all ramets, showed that the distribution of suitability categories for new hosts did not differ from that of old hosts (Fig. 4, A, C and E; Chi square goodness of test: *Ho*: $\chi 2=0.422$, $P=0.516$, $df=1$; *Hf*: $\chi 2=1.385$, $P=0.239$, $df=1$; and *Hm*: $\chi 2=0.045$, $P=0.831$, $df=1$) Just 26- 36 percent of the ramets found a suitable host. But if one considers the consequences of clonal propagation for the ortet as a whole, the picture is more positive. The suitability of the host for the entire ortet did change after ramet production: in all, it resulted in a higher proportion of suitable hosts for ortets (Chi square goodness of test: *Ho*: $\chi 2=8.595$, $P=0.003$, $df=1$; *Hf*: $\chi 2=65.751$, $P=0.000$, $df=1$, and *Hm*: $\chi 2=64.090$, $P=0.000$, $df=1$). In 35 and 46 percent of the ortets that produced ramets, at least one of its ramets climbed a suitable host (Fig. 6, B, D and F).

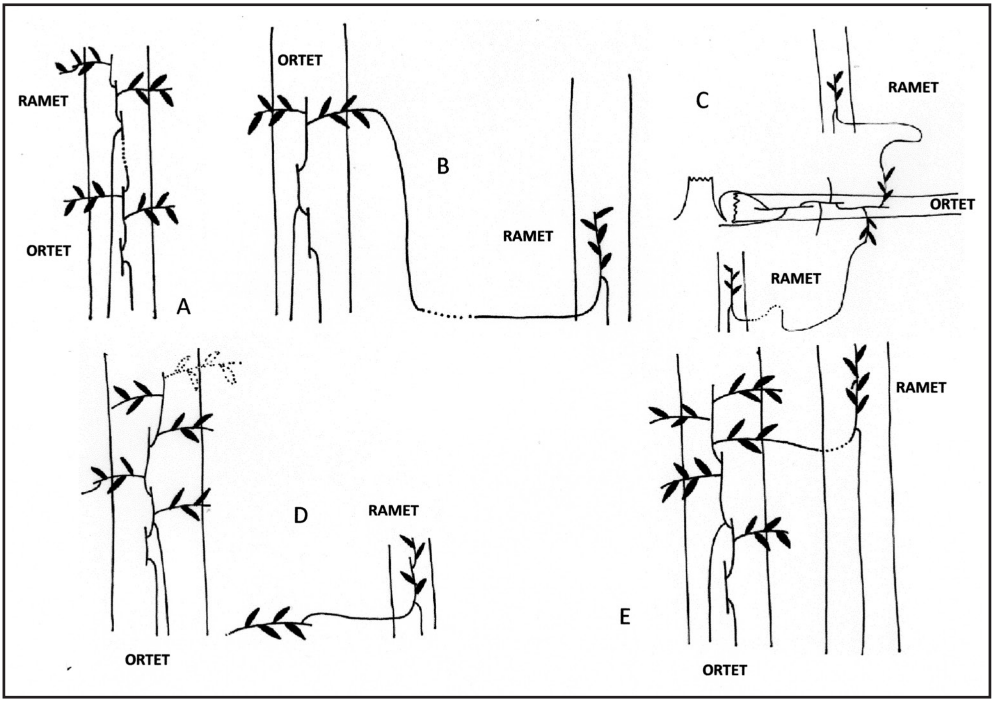


Figure 5. Cloning types: **A)** An orthotropic branch dies off (dotted line) and the plant survives in two parts. **B)** Plagiotropic branch becomes a flagellar shoot which climbs up a new host. After the climber produces a new anchoring root, the ramet separates. **C)** Plant falls (with or without host). Plagiotropic branch produces a stolon that climbs up new hosts, and eventually separate. **D)** Plagiotropic branch breaks off and survives by producing a stolon that climbs up a new host. **E)** Same case as B, but the shoot finds a new host without touching the soil. (Drawing by M.P. Balcázar-Vargas).

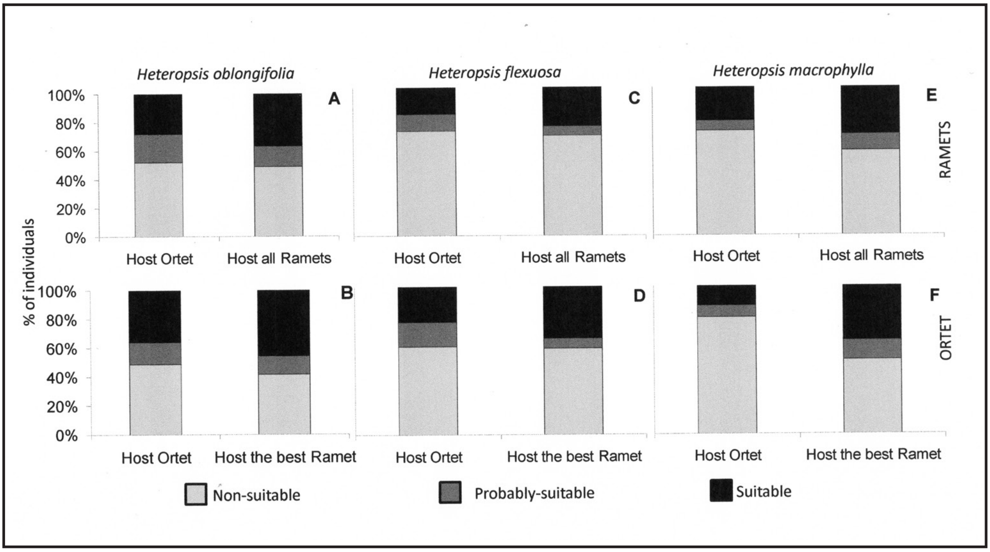


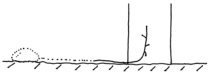
Figure 6. Suitability of host ortet and the host of the ramets in three *Heteropsis* species. Upper panels show host suitability for individual ramets (shoots) that were produced and searched for a new host. Lower panels show host suitability for the entire ortet, such that if at least one of the ramets is climbing a suitable host, the host of the ortet would be called suitable. See text for results of statistical tests.

Discussion

Host Size Distributions

The majority of *Heteropsis* seedlings climbed up in very small and non-suitable hosts. Many 'hosts' of our study species were in fact herbs, tree seedlings or dead plants. Up to 81 percent of the hosts of *Heteropsis* recruited seedlings are non-suitable for the seedlings to complete their life cycle. This finding is consistent with the results of various studies on host tree characteristics of tendril lianas (Putz 1984, Putz & Holbrook 1991, Nabe-Nielse 2001, Sakai et al. 2002). However, tendril lianas have hardly been seen climbing up on herbs (Vleut & Pérez-Salicrup 2005), unlike *Heteropsis* seedlings. Maybe this difference is because most lianas are ≥ 50 cm in height when before they start searching for the first host (Gerwing 2004, Vleut & Pérez-Salicrup 2005). In contrast to *Heteropsis* seedlings, most of the adults of the two canopy species *H. flexuosa* and *macrophylla* were growing on hosts ≥10 cm DBH.

In a recent study, Lozano-Orihuela and Waechter (2010) reported that host size distributions of secondary hemiepiphytes in southern Brazil were similar to the ones we found for *Heteropsis* adults. As they only took into account individuals with roots or stems at breast height, they probably missed most of the juveniles and all of the seedlings of the

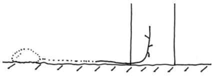


hemiepiphytes. Therefore, their results are only comparable to the host size distribution of adults of H *flexuosa* and *H. macrophylla* from our study Knab-Vispo et al. (2003) found comparable results on the host size distribution of large individuals of all *Heteropsis* species in a Venezuelan forest. Also in this case, large *Heteropsis* individuals were more common on medium-sized host trees (20-49 cm DBH) than expected based on the size distribution of all trees in the community. In all, both studies are in accordance with our findings that the host size distribution of adult individuals of secondary hemiepiphytes includes more large trees compared to that of all trees in the forest (Figure 3, C, F I).

The Initial Search For A Suitable Host

We observed that searching behavior of the stems or shoots was often erratic: they were growing in random directions and could also change direction without noticeable cue (e.g., changing light conditions, physical obstruction). Also, virtually no seedling was growing in a straight line and we sometimes found clumps of seedlings together which were derived from seeds of the same infructescence, growing in very different directions. Although these are observations and we lack measurements and statistical tests to determine whether the growing direction of seedlings was in fact random, these preliminary observations do seem to provide some evidence suggesting that host searching is random. In any case, our observations contrast those of Strong and Ray (1975) on the hemiepiphyte *Monstera gigantea*. They found that seedlings of this species grow towards the same dark spots in the forest (large tree trunks; Ray 1976). If growth of our *Heteropsis* seedlings species would be governed by the same mechanism of skototropism, we would have found most of the stems of different recruited seedlings of the same infructescence growing in the same direction, instead of radiating directions. Also, in that case would have expected to find *Heteropsis* seedlings to climb the parent tree or large trees and not the smallest hosts in the forest. In all, our results seem to suggest that *Heteropsis* seedlings climb up a randomly found, nearby host, and that they adopt a random searching strategy instead of one directed by skototropism.

Finding a suitable host may represent a serious regeneration bottleneck for our study species. This bottleneck is mainly caused by two factors. First, the leafless non-climbing seedlings experience a high mortality risk and thus cannot survive for long periods. We estimate that these non-climbing seedlings will survive sufficiently long to reach spots within 1 m of their place of germination spot. Second, the density of suitable host trees is very low. In our study area, there are only 0.06 suitable trees per m2 for *H. flexuosa* and *H. macrophylla* and 0.30 per m2 (Phillips & Miller 2002) for *H. oblongifolia*. Thus, the chances to find a suitable host are slim. This is reflected by the very low proportion of recently recruited seedlings that climb in a suitable host for the first time. Even when *Heteropsis* seedlings germinate close to the supposed host tree of their mother plant, most of them will climb up in a non-suitable host. In contrast, seedlings of *Monstera* were found to grow back to the host tree of their mother plant (Ray 1976). The apparent random searching behavior of *Heteropsis* seedlings and the resulting high fraction of climbing seedlings on non-suitable hosts is intriguing and requires further study.



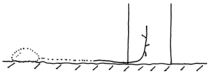
THE CONTINUED QUEST

Recently recruited *Heteropsis* seedlings that have climbed their first host (R seedlings) are more often present on a non-suitable host compared to the established seedlings (P category). This difference can be explained in two ways: (1) a proportion of the established seedlings (P) have already changed host and are now present on their second or third host, and/or (2) recruited seedlings on non-suitable host have a higher chance to die compared to those on suitable hosts. To understand the contributions of these possible causes in explaining the higher proportion of suitable hosts for established seedlings, dynamic data on survival and host-changing of climbing seedlings is required.

As the majority of the *Heteropsis* seedlings climbed non-suitable hosts, these plants are obliged to search for a new host. Clonal propagation allows *Heteropsis* to move from a non-suitable host to a suitable one. Every year, between 0.6 and 2.4 percent of the *Heteropsis* individuals sent out branches – ramets – that were searching for new hosts; most of them climbed non-suitable host. However, the suitability of the host for the entire ortet did change after ramet production, because in 35 to 46 percent of the cases, at least one of the ramets climbed a suitable host. This means that, these long-lived plants probably need to produce a large number of ramets to guarantee that one of them finds a suitable host, which allows the genetic individual as a whole to reproduce. Our results suggest that the host tree searching does not stop at the seedling category. It appears to be a repetitive trial and error searching method through clonal propagation, until the plant reaches the understory (*H. oblongifolia*) or the canopy (*H. flexuosa* and *macrophylla*).

The ramet production in *Heteropsis* is a consequence of the constraints of the climbing strategy. In this way the *Heteropsis* ortet moves from one host to another subdividing itself into initially dependent but later independent ramets. In our study species, we observed that the connection between the ramet and ortet is most often lost within two years (M.P. Balcázar-Vargas, personal observations). A *Heteropsis* ortet which succeeds in establishing ramet in a suitable host has effectively increased its chances of reproduce. Therefore, the expected life-span is increased, first because the risk of mortality is spread over a number of ramets, and secondly because the fate of the genet is uncoupled from the fate of the tree it first climbed. This was found to be the case for two species of tropical vines by Peñalosa (1984).

We found clear differences between *H. oblongifolia* and the other two species. *H. oblongifolia* reaches reproductive size already at 1.5 m height, whereas the other two species do so in higher strata in the forest. Therefore, a larger proportion of trees in the forest are suitable hosts for *H. oblongifolia* as small trees are more abundant (e.g., Duivenvoorden 1994, Phillips & Miller 2002). As a result, the proportion of established seedlings and juveniles in suitable hosts is higher than that of the other two species. However, there may be another reason for this difference: *H. oblongifolia* produces ramets at a higher rate and the more vigorous clonal propagation of this species may increase the chance that established seedlings and juveniles are present on suitable hosts.



How would *Heteropsis* individuals sense that a host is non-suitable? We observed that many *Heteropsis* individuals produced flagellar shoots to the ground before they reached the top of a non-suitable host. This behavior has been documented for other species in the Araceae family (Ray 1976, 1992; Andrade & Mayo 1998, 2000). Ray (1976) argues that this switch seems to occur only when a hemiepiphyte is climbing on a host that is too small. In general, the change from one host to another is thought to be triggered by sensitive stimuli and contact with supports (Braam 2005). Clearly, further studies are needed to test what triggers the production of shoots in *Heteropsis* and other secondary hemiepiphytes.

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Drawing of a *Heteropsis macrophylla* seedling (Drawing by Maria Teresa Vargas-Paz).

Chapter 3

What drives the vital rates of secondary hemiepiphytes? A first assessment for three species of Heteropsis (Araceae) in the Colombian Amazon

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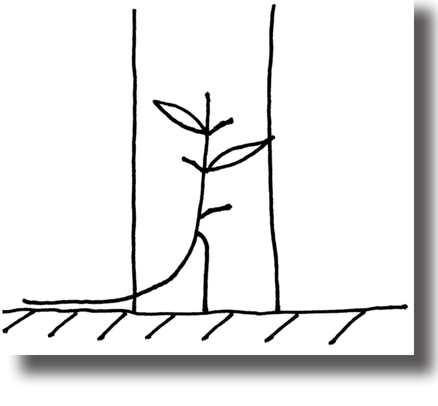

What drives the vital rates of secondary hemiepiphytes? A first assessment for three species of Heteropsis (Araceae) in the Colombian Amazon

ABSTRACT

Secondary hemiepiphytes rely on other plants (hosts) to grow vertically. After germinating on the forest floor, their seedlings search a host to ascend. Little is known about the factors determining vital rates of secondary hemiepiphytes. We recorded survival, growth, reproduction and vegetative propagation of three *Heteropsis* species in three permanent plots in the Colombian Amazon to quantify and evaluate what drives their vital rates. We found a gradual increase in stem length, leaf size, number of roots and number of plagiotropic branches with increasing height of *Heteropsis* individuals on their hosts. Survival of leafless non-climbing seedlings was very low (28 % annually), increasing substantially (84 - 94 %) once the seedling had ascended a host. The three *Heteropsis* species presented slow height growth rates (ca. 2 - 8 cm / year) with large variation, while a substantial percentage (31 – 62 %) did not grow or shrunk. When considering only the positive growth values, we found that growth rates in upper height increased with initial upper height, crown exposure and number of absorbing roots. The chance of reproduction increased with height and the number of plagiotropic branches in two of the three species. The probability of segregating into two segments increased with stem length. The probability that an individual produced a ramet and change the host was significantly higher in non-suitable host. Vegetative propagation allows *Heteropsis* to survive hydraulic failure, and acts as a dispersion-propagation strategy to find a suitable host and reach the canopy again after falling. The very high mortality rate of non-climbing seedlings of secondary hemiepiphytes may constitute an important demographic bottleneck. These species have very slow growth rates; suggesting that when they attain the canopy they may have a remarkable old age. Once plants have reached the canopy, their longevity is largely determined by the survival probability of the host tree.

RESUMEN

Las hemiepífitas secundarias dependen de otras plantas (hospederos) para crecer verticalmente y alcanzar el sub-(dosel). Después de germinar en el suelo del bosque, sus plántulas buscan un hospedero para ascender. Poco se sabe sobre los factores que determinan las tasas vitales de las hemiepífitas secundarias. Determinamos la supervivencia, el crecimiento, la reproducción sexual y vegetativa de tres especies de *Heteropsis* en tres

parcelas permanentes en la Amazonia colombiana, para cuantificar y evaluar lo que determina sus tasas vitales. Se encontró un aumento gradual de la longitud del tallo, tamaño de las hojas, número de raíces y número de ramas plagiotrópicas en los individuos de *Heteropsis* conforme aumentan en altura en sus hospederos. La supervivencia de las plántulas que aun no habían trepado, fue muy baja (28% anual), ésta aumenta considerablemente (84 - 94%) una vez que las plántulas han ascendido a un hospedero. Las tres especies de *Heteropsis* presentaron tasas de crecimiento en altura muy lentas (ca. 2 a 8 cm / año) con una gran variación, mientras que un sustancial porcentaje (31 - 62%) no creció o redujo su tamaño. Si se consideran solamente los valores positivos de crecimiento, se encontró que las tasas de crecimiento en altura superior aumentaron conforme a la altura inicial superior, la exposición de la corona y el número de raíces absorbentes. La probabilidad de reproducción aumentó con la altura y el número de ramas plagiotrópicas en dos de las tres especies. La probabilidad de segregarse en dos segmentos aumentó con la longitud del tallo. La probabilidad de que un individuo produce un ramet y cambia de hospedero fue significativamente mayor en hospederos no adecuados. La propagación vegetativa les permite a los individuos de *Heteropsis* sobrevivir fallos hidráulicos, y actúa como una estrategia de dispersión - propagación para encontrar un hospedero adecuado y al alcanzar el dosel de nuevo después de caer. Las altísimas tasas de mortalidad de las plántulas que aún no han trepado a un hospedero pueden constituir un importante cuello de botella demográfico para las hemiepífitas secundarias. Estas especies tienen unas tasas de crecimiento muy lentas; lo que sugiere que cuando alcanzan el sub-(dosel) sus individuos pueden tener una edad notable. Una vez que las plantas alcanzan el dosel, su longevidad es determinada en gran medida por la probabilidad de supervivencia de los árboles hospederos.

Key words: *clonal or vegetative propagation, growth, host suitability, shrink, survival*.

INTRODUCTION

Secondary hemiepiphytes are characteristic elements of tropical forests (Williams-Linera & Lawton 1995), with approximately 700 to 1000 species belonging to the families Araceae, Marcgraviaceae and Cyclanthaceae (Croat 1988; Williams-Linera & Lawton 1995). They rely on other plants (hosts or phorophytes) to grow vertically. Secondary hemiepiphytes have a very distinct life cycle compared to many other plant growth forms in tropical forests: they germinate on the forest floor and seedlings search a host by growing to dark spots (skototropism, Strong & Ray 1975) or by searching randomly (Chapter 2). Once a shoot tip of a seedling has reached a host, it climbs up using adventitious anchoring roots (Wilder 1992; Romero 1994). When the plant is attached, absorbing roots are formed growing downwards. When these roots reach the soil, the lower part of the stem dies. The plant continues to grow up, producing orthotropic (vertical) an plagiotropic branches (horizontal branches bearing leaves in planes along each axis) and more absorbing roots, and gradually shedding its lower parts (Putz & Holbrook 1986; Knab-Vispo et al. 2003; Plowden et al. 2003). Some

species later lose the root connection to the ground, while others do not (Putz & Holbrook 1986) (Fig. 1 A-G). Secondary hemiepiphytes reproduce sexually once they have reached a threshold size or height on the host and this implies that small host trees are not suitable (Chapter 2). Some species are also capable of vegetative reproduction (Ray 1976, 1992, Andrade & Mayo 1998, 2000), which can be a strategy to encounter a suitable host after falling or climbing a non-suitable host (Chapter 2). Just like lianas and rattans, secondary hemiepiphytes can survive after falling down from a tree (Peñalosa 1984, Putz 1984, Putz 1990a, Chapter 2), an ability that distinguishes them from most other rain forest plants.

Heteropsis species can be expected to achieve high rates of extension growth as shade-tolerant lianas and rattans (Bøgh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, Schnitzer 2005), because: First, their stems have only a limited support function and biomass allocated to them can be invested in stem extension, rather than in stoutness (Bell et al. 1988, Darwin 1867, Putz 1984, den Dubbelden & Verburg 1996). Therefore, it can be expected that secondary hemiepiphytes grow fast in height as lianas or rattans, since they make use of the surrounding vegetation to ascend. Secondly, the epiphytes' habitat is very dynamic. Therefore, it might be expected that these plants respond to this selective pressure, showing high growth rates, an early reproductive maturity and abundant seed production (Benzing 1978). Third, secondary hemiepiphytes have absorbing roots that allow them to connect to the soil and uptake water and nutrients continuously (Croat, 1981). I expected that as these plants ascend to the canopy, growth rates increase. Since, they will have more and thicker absorbing roots, more plagiotropic branches and greater access to light; so they can obtain more water and nutrients and photosynthesize more. As a consequence, growth rates are expected to increase with height on the host.

The particular life history of secondary hemiepiphytes also has implications for size-dependent patterns of mortality rates. While in the non-climbing stage, small seedlings may be highly vulnerable to mortality by falling debris (Clark & Clark 1989); the mortality risk is likely considerably lower once they have ascended a host tree. A sudden drop in mortality risk is therefore expected from non-climbing to climbing individuals, especially when the latter have climbed a suitable (i.e. large) host tree. As a shoot climbs a tree, it will generally be moving into regions of gradually less disturbance by falling debris (Ray 1990).

While there have been recent advances in quantifying vital rates of lianas, vines, rattans and epiphytes (e.g. Nabe-Nielsen 2004, Zotz 2005, Gilbert et al. 2006, Kouassi et al. 2008, Binh 2009), such knowledge is very limited for hemiepiphytes (Williams-Linera & Lawton 1995). So far, some studies have dealt with individual performance of primary hemiepiphytes, including the well-known strangler figs (Todzia 1986, Michaloud & Michaloud-Pelletier 1987, Putz & Holbrook 1986, Daniels & Lawton 1991), but secondary hemiepiphytes have remained understudied. Here we report on size-dependent patterns in vital rates of three secondary hemiepiphytes of the genus *Heteropsis* in a Colombian rainforest. Absorbing roots of some *Heteropsis* species are used throughout the Amazon Basin for house construction, basketry, traps and furniture (cf. Bennett 1992, Paz y Miño et al. 1995, Knap-Vispo et al. 2003, Balcázar-Vargas & van Andel 2005). In order to design sustainable harvesting levels for these economically valuable species, we need to know more about their vital rates. To our knowledge, this is the first study providing such insights into hemiepiphyte ecology. We address the following questions: How do light conditions, plant size and architecture of secondary hemiepiphytes change with height on host trees? What factors govern vital rates (survival, growth, vegetative propagation and sexual reproduction) of these species? Do growth rates differ between hemiepiphytes on suitable and non-suitable hosts (i.e. large host trees vs. small host trees)? Our results provide basic insights into growing conditions and vital rates of secondary hemiepiphytes, and on factors governing their performance.

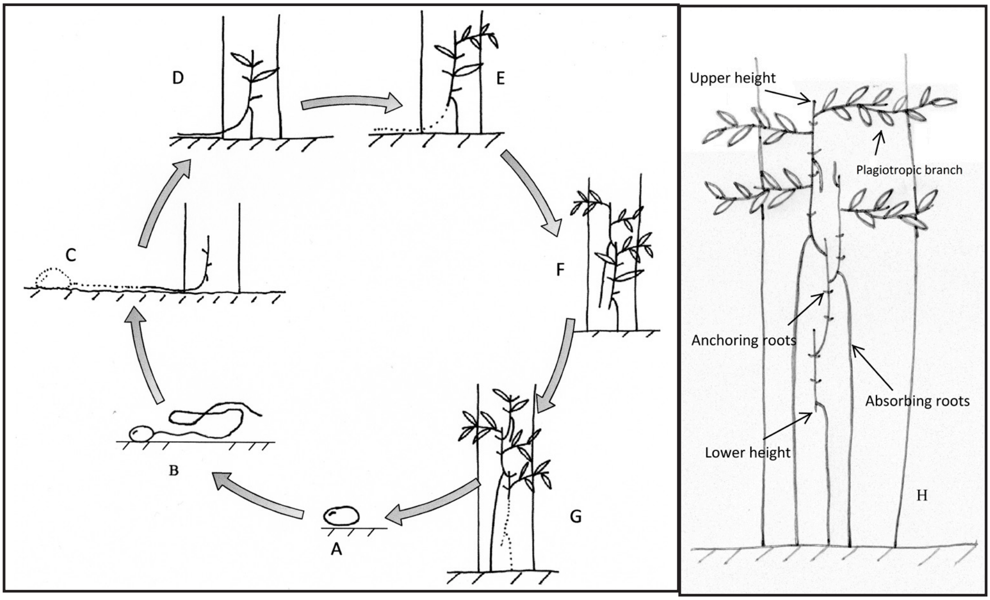

Figure 1. The life cycle and some structural details of a *Heteropsis* individual. **A)** Seed on the forest floor. **B)** Seed germinates. **C)** Seedling finds a host and adheres to it. **D)** Absorbing root sprouts and grows downward until it reaches the soil. **E)** Stem loses connection to the soil. **F)** and **G)** Hemiepiphyte grows and becomes reproductive. Lower stem senesces together with the lowest root(s). **H)** Structural details of *Heteropsis* species. Illustration by M.P. Balcázar-Vargas.

STUDIED SPECIES

Here we studied three species of the genus *Heteropsis* (Araceae). *Heteropsis flexuosa* (Kunth) G.S. Bunting, *H. macrophylla* A.C. Sm and *H. oblongifolia* Kunth are three secondary hemiepiphytes distributed along the Amazon and *H. oblongifolia* much of Central America (Croat 1988). These species differ in their maximum height reached on host trees: 14 m for *H. oblongifolia*, 25 m for *H. flexuosa* and 35 m for *H. macrophylla*. They also differ in the height at which they become reproductive: *H. flexuosa* and *macrophylla* produce inflorescences at ≥ 10 m while *H. oblongifolia* at ≥ 1.5 m (Chapter 2).

METHODS

STUDY SITE

Field work was conducted from February 2007 to September 2009 at El Zafire Biological research station (ZBS) of the Universidad Nacional de Colombia, located in the southern-most part of the Colombian Amazon at 4°0’ S, 69°53’ W with an elevation of approximately 80 m asl (Fig. 3 in Chapter 1). The mean annual temperature is 26 °C with a relative humidity of 86 % (Jiménez 2007). This area has sandy soils and four major forest types: tierra firme, floodplain, white sand and transition forest (Peñuela & Alvarez 2006). All are old-growth forests with no evidence of human disturbance except for hunting. Specimens of all species were collected and identified at the Herbario Nacional Colombiano (COL), where they are stored as MPB 1615 (*H. flexuosa*), MPB 1614 (*H. macrophylla*) and MPB 1604 (*H. oblongifolia*).

SAMPLE DESIGN AND FIELD MEASUREMENTS

We conducted the study in three plots (0.7, 1 and 4 ha) in undisturbed tierra firme forest; two of which are permanent plots included in the RAINFOR network (Peñuela & Alvarez 2006). In these plots, we categorized *Heteropsis* individuals into three life cycle stages: seedlings (P), juveniles (J) and adults (A), based on the upper height on the host and the minimum height at which a plant became reproductive. *H. flexuosa* and *macrophylla* were considered to be seedlings if they were searching for a host (Category B in Fig. 1) or climbing a host to ≤1 m height (Categories C-E). Juveniles were defined as having an upper height of 1-10 m and adults’ ≥10 m. In *H. oblongifolia*, seedlings were <50 cm tall; juveniles had an upper height of 0.5-1.5 m, and adults ≥1.5 m, the height at which reproduction started.

In 2007, we located, tagged and measured adults, juveniles and seedlings of the three *Heteropsis* species in the three plots, following the standard practice for nested plot design (Elzinga et al. 2001). For each *Heteropsis* individual, we measured its upper and lower height on the host tree (Fig. 1, H), employing a fiberglass telescopic rod or a measuring tape using climbing techniques. With permanent paint we marked the upper and lower height of the hemiepiphyte on its host tree. We estimated plant length as upper height minus lower height. We used upper height and length as complementary measures to explain the variation in the vital rates. In order to calculate leaf size (cm2), we recorded the leaf length and width (cm) of three leaves on the highest plagiotropic branch. *Heteropsis* leaves have an oval form, so the formula to calculate leaf size was:

$$\textit{leaf size} = (\pi * \textit{leaf length} * \textit{leaf width})/4$$

We tagged and recorded the total number of absorbing roots and the maturity state with the help of local experts (Fig. 1, H) and followed the production of absorbing roots for 28

months (*H. flexuosa*) and 24 months for (*H. macrophylla* and *oblongifolia*). Light conditions of each individual were assessed using the crown exposure index (CE; Dawkins & Field 1978, Clark & Clark 1992, Poorter et al. 2005), with modifications according to the life form of secondary hemiepiphytes: 1 = no direct light –canopy closed-; 2 = slight lateral direct light –small sizes canopy openness-; 3 = some lateral direct light –small sizes canopy openness-; 4 =partial overhead light; 5 = almost direct overhead light or emergent crown with direct light from all directions.

In 2009, we counted the total number of plagiotropic branches per plant. We traced the reproductive status for 132 (*H. flexuosa*), 93 (*H. macrophylla*) and 109 (*H. oblongifolia*) individuals, every month, during two years. We recorded the inflorescence and infrutescence production of *H. flexuosa* from 7 m; *H. macrophylla* from 8 and *H. oblongifolia* from 1 m on hosts. Furthermore, we recorded and tagged whether individuals had a branch that climbed up another host. If these branches had lost connection with its parent ('ortet') at the next census, we recorded this 'ramet' as a new individual, produced by vegetative propagation. Ramet production was recorded in 2008 and 2009. To facilitate the interpretation of branching and ramet production, we made drawings of all measured individuals every year. We recorded fallen individuals and as well as occurrence of each of the five types of vegetative reproduction that we described earlier (Chapter 2).

The measurements were repeated in June–September 2008 and 2009, during which the survival and growth of the ortets and ramets was assessed. The upper and lower heights were measured; the roots maturity and the crown exposure index were assessed. In total, we measured 758 individuals of *H. flexuosa*, 674 of *H. macrophylla* and 647 of *H. oblongifolia*.

Finally, we categorized hosts as 'non-suitable' or 'suitable', based on the minimum height at which the three *Heteropsis* species reproduce, the host's height, inclination, whether it was alive or dead and the expected height growth rates of host trees (see Chapter 2).

Statistical Analysis

Change In Plant Size And Architecture With Height

We used logarithmic regressions to determine the relation between length and upper height. Length was log-transformed to normalize the residuals to meet the assumptions of normality and equal variance. Multinomial logistic regression was used to analyze the relation between the upper height of the plant on a host and the crown exposure (CE). This analysis predicts CE at first census as a function of hemiepiphyte upper height. The probability of a hemiepiphyte (p) being in a certain CE class i (i= 1, 2, 3, 4, 5) is a function of its height $f\,i\,(h)$ (Poorter et al. 2005). To find out whether there was a relation between length or upper height and number of absorbing roots, Spearman's correlations were carried out. Furthermore, we evaluated the relation between the number of plagiotropic branches

and the upper height or length using regressions. Finally, we assessed the relation of leaf size versus the upper height of the plant using logarithmic regression.

Calculation Of Vital Rates

We pooled data on vital rates (survival (σi), growth (gi) and fecundity (fi)) of the three plots as these did not differ among plots (One-Way ANOVA; $P \geq 0.05$). We decided to calculate annual vital rates based on two years of observations (i.e. two inter-census intervals), as our study species grew very slowly and no differences between years were found. Size-dependent survival was related to the initial upper height and suitability of the host using forward multiple logistic regressions. In this analysis we only included those individuals with upper heights smaller than the maximum height of non-suitable hosts (*H. oblongifolia*: 1.5 m; *H. flexuosa*: 8.4 m; *H. macrophylla*: 6.0 m). If variation in survival was not significantly explained by host suitability, we performed a simple logistic regression for all individuals, thus including the full height range.

Rates of growth in upper height were found to be negative for a large share of the individuals, often related to damage, or a partial fall of the upper orthotropic branches. Since we were interested in factors governing positive growth in upper height, we performed analyses on a subset of individuals with positive growth rates. First, we performed an analysis of covariance (ANCOVA) to evaluate if positive growth rate differed significantly between suitable and non-suitable hosts. Again, this was done for those individuals with upper height smaller than the maximum height of non-suitable hosts (*H. oblongifolia*: 1.5; *H. flexuosa*: 8.4 m; *H. macrophylla*: 6.0 m). If the interaction between the upper height and suitability was not significant (≥0.05), a full-factorial ANCOVA was performed. If suitability was not significant (≥0.05), a second analysis was done for all individuals. This was a forward multiple linear regression over the entire height range to evaluate whether crown exposure, total number of absorbing roots (immature and mature) could explain variation in upper height growth. In these analyses, upper height growth rate was log-transformed to meet the assumptions of normality and equal variance.

After checking for differences between years in probability of reproduction (multiple logistic regressions) we assessed whether reproduction probability (during two years) depended on the number of plagiotropic branches and upper height, using multiple logistic regressions. To assess the relation between the number of inflorescences, upper height and the year, forward multiple linear regressions were performed. The number of inflorescences was log-transformed to meet the assumptions of normality and equal variance.

We evaluated the probability of two types of vegetative propagation: segregating in two segments on the same host and changing host through ramet production (Chapter 2). To see whether the probability of vegetative propagation was size-dependent (length or upper height) and related to the suitability of the host, we applied forward multiple logistic regressions. The maximum upper height included in this analysis

was restricted to the maximum height of non-suitable hosts (*H. oblongifolia*: 1.5 m; *H. flexuosa*: 8.4 m; *H. macrophylla*: 6.0 m). To determine whether the probability of falling from or with the host differed during the two years of observation, we used McNemar's test. We assessed whether there were differences between the non-suitable and suitable host by using a Chi-square test. If there were no differences, we performed a logistic regression for both years together. Furthermore, we calculated the probability that a fallen individual produced a climbing ramet and divided in two, plus the probability that the ramet climbed up a non-suitable or suitable host. All statistical analyses were conducted using the software SPSS 16 (SPSS Inc., Chicago, Illinois, U.S.A.).

RESULTS

CHANGES IN PLANT SIZE AND ARCHITECTURE WITH HEIGHT

Our study species reached heights on a host up to 14 m for *Heteropsis oblongifolia* (*H. oblongifolia*, understory species) to 35 m for *Heteropsis macrophylla* (*H. macrophylla*, canopy species). The maximum length of adult individuals ranged from 6 m (*H. oblongifolia*) to 23 m (*H. macrophylla*). Plants that reached a higher upper height on hosts also tended to be longer. These relations between Ln (length) and upper height were quite strong (Fig. 2). Individuals with much lower length than expected based on their upper height have most likely segregate into two segments.

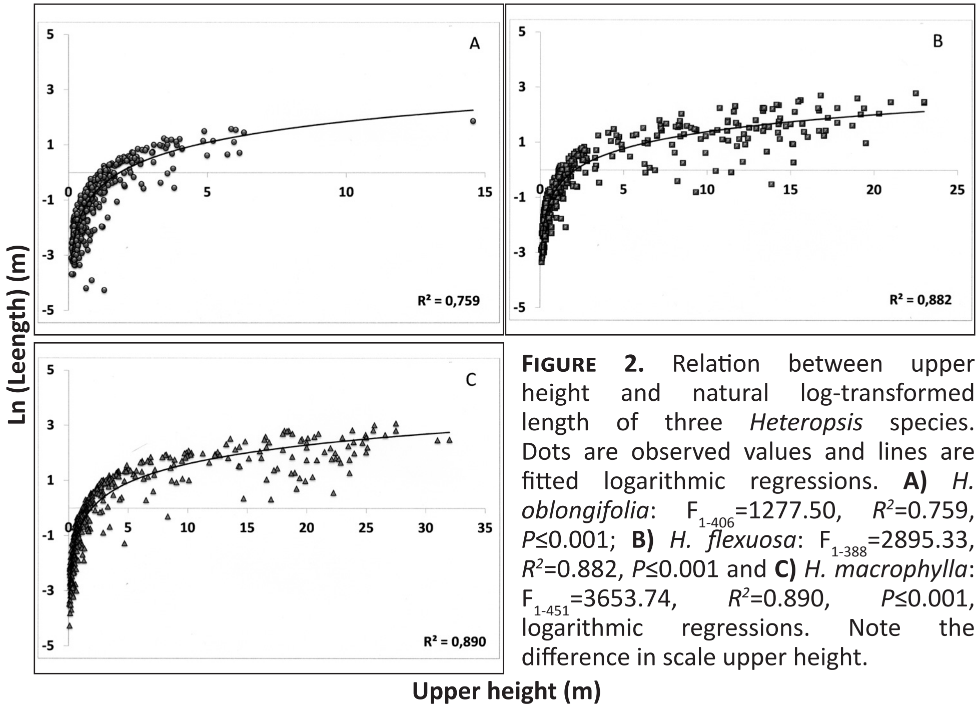

FIGURE 2. Relation between upper height and natural log-transformed length of three *Heteropsis* species. Dots are observed values and lines are fitted logarithmic regressions. **A)** *H. oblongifolia*: $F_{1\text{-}406}$=1277.50, R^2=0.759, $P \le 0.001$; **B)** *H. flexuosa*: $F_{1\text{-}388}$=2895.33, R^2=0.882, $P \le 0.001$ and **C)** *H. macrophylla*: $F_{1\text{-}451}$=3653.74, R^2=0.890, $P \le 0.001$, logarithmic regressions. Note the difference in scale upper height.

The maximum number of absorbing roots per plant (mature and immature) was 12, 11 and 6 for *H. flexuosa*, *H. macrophylla* and *H. oblongifolia*, respectively. The average number of absorbing roots of adult individuals was 2.3±0.1 (*H. oblongifolia*), 2.8±0.2 (*H. flexuosa*) and 3.1±0.2 (*H. macrophylla*). The number of absorbing roots increased slightly with length (Table 1). Production of absorbing roots was also low: 16 roots were produced in 28 months in 3.7 ha for *H. flexuosa* (N=95), while *H. macrophylla* produced just 6 roots in 24 months in 21.7 ha (N= 29).

Table 1. Relation between the upper height, length and the number of absorbing roots. Spearman's correlations were conducted for the three *Heteropsis* species. Significance: ** Correlation is significant at the 0.01 level (2-tailed).

Species		***H. oblongifolia***	***H. flexuosa***	***H. macrophylla***
		# of absorbing roots		
Upper height	*ρ*	0.357**	0.567**	0.494**
	P	≤0.001	≤0.001	≤0.001
	N	412	183	521
Length	*ρ*	0.468**	0.673**	0.554**
	P	≤0.001	≤0.001	≤0.001
	N	411	180	510

The maximum number of plagiotropic branches was 12, 30, and 35 for *H. oblongifolia*, *H. macrophylla* and *H. flexuosa* respectively. For adults, the average number of branches was four (*H. oblongifolia*) to 10 (*H. flexuosa*). In general, the number of plagiotropic branches increased with upper height in the three species. From 12 m upper height, the number of these branches increased more rapidly in *H. macrophylla*, but *H. oblongifolia* did not show a strong relation (Fig. 3). The number of plagiotropic branches increased linear with increasing length for *H. oblongifolia* and *macrophylla* and quadratic for *H. flexuosa* (*H. oblongifolia*: F_{1-403}=126.89, R^2=0.240, P≤0.001; *H. macrophylla*: F_{1-454}=227.41, R^2=0.334, P≤0.001, linear regressions; *H. flexuosa*: F1-436=935.31, R^2=0.696, P≤0.001, quadratic regression). Thus, the number of branches increased with upper height and length.

Leaf size increased logarithmically with upper height: *H. flexuosa* and *macrophylla* showed a steep increase in the leaf size up to 2 m upper height, whereas leaf size of plants of over 4–5 m did not increase much more (Fig. 4). The maximum leaf size of the three species varied from 140 to 160 cm2. *H. oblongifolia* had the largest leaf size and variation in leaf size in relation to the upper height.

In brief, our study species showed gradual increase in length, leaf size, number of roots and plagiotropic branches as they climbed up host trees.

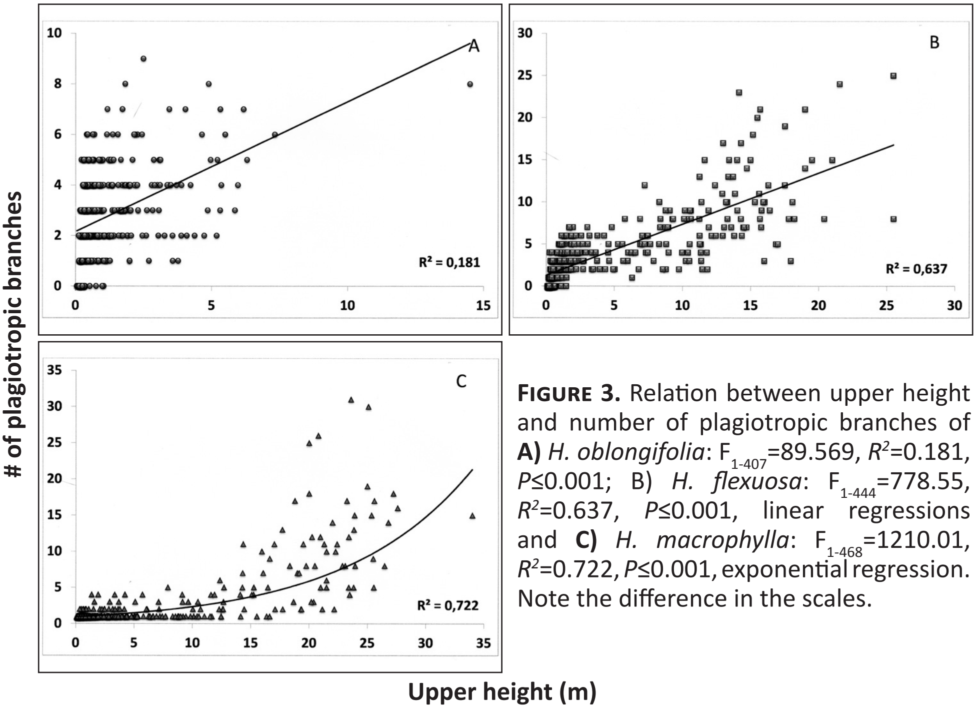

FIGURE 3. Relation between upper height and number of plagiotropic branches of **A)** *H. oblongifolia*: $F_{1\text{-}407}=89.569$, $R^2=0.181$, $P\leq0.001$; B) *H. flexuosa*: $F_{1\text{-}444}=778.55$, $R^2=0.637$, $P\leq0.001$, linear regressions and **C)** *H. macrophylla*: $F_{1\text{-}468}=1210.01$, $R^2=0.722$, $P\leq0.001$, exponential regression. Note the difference in the scales.

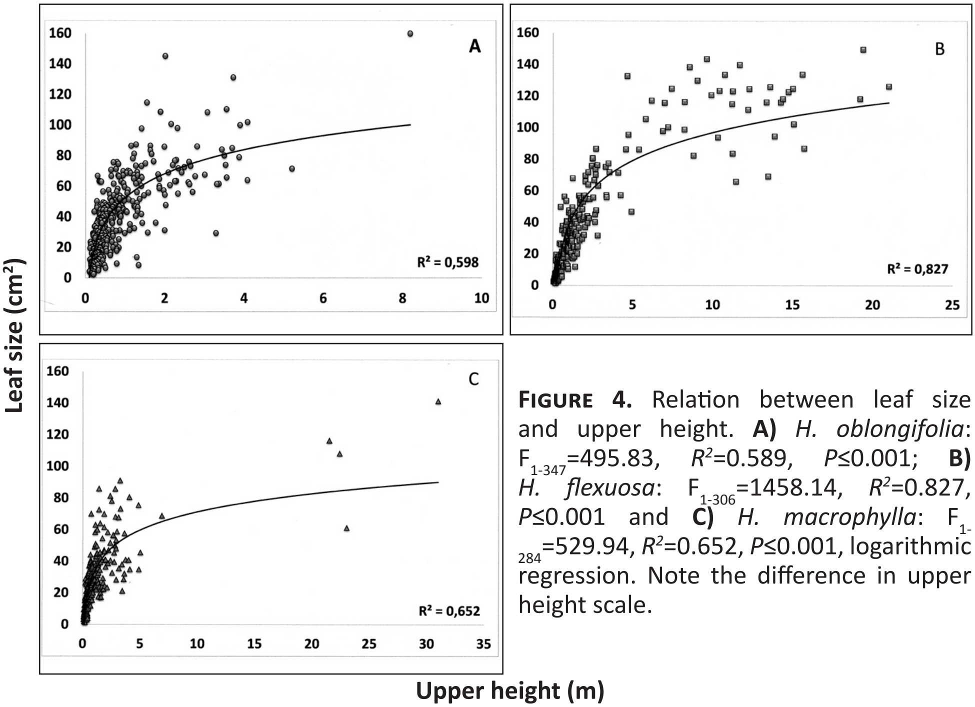

FIGURE 4. Relation between leaf size and upper height. **A)** *H. oblongifolia*: $F_{1\text{-}347}=495.83$, $R^2=0.589$, $P\leq0.001$; **B)** *H. flexuosa*: $F_{1\text{-}306}=1458.14$, $R^2=0.827$, $P\leq0.001$ and **C)** *H. macrophylla*: $F_{1\text{-}284}=529.94$, $R^2=0.652$, $P\leq0.001$, logarithmic regression. Note the difference in upper height scale.

CROWN INDEX VS. UPPER HEIGHT

Crown exposure index increased strongly and non-linearly with upper height for the two (sub)-canopy species (*H. macrophylla* and *flexuosa*; Fig. 5 B and C), while almost no increase was observed for the understory species (*H. oblongifolia*; Fig. 5 A). The largest increase in crown exposure occurred between 9.5 and 17 m height (Fig 5 B and C). In each of the three study species a large share of individuals (43 - 50 %) was strongly shaded (CE 1). Only 1.4 - 5.4 % of *H. flexuosa* and *macrophylla* adult plants received almost direct overhead light (CE 5). Plants at 1 m upper height had an average CE of 1.48 - 1.61 for all species, and those of 10 m an average of 2.02 (*H. flexuosa*) and 2.51 (*H. macrophylla*). When reaching the forest canopy (30 m), *H. macrophylla* individuals experienced a crown exposure of 4.9.

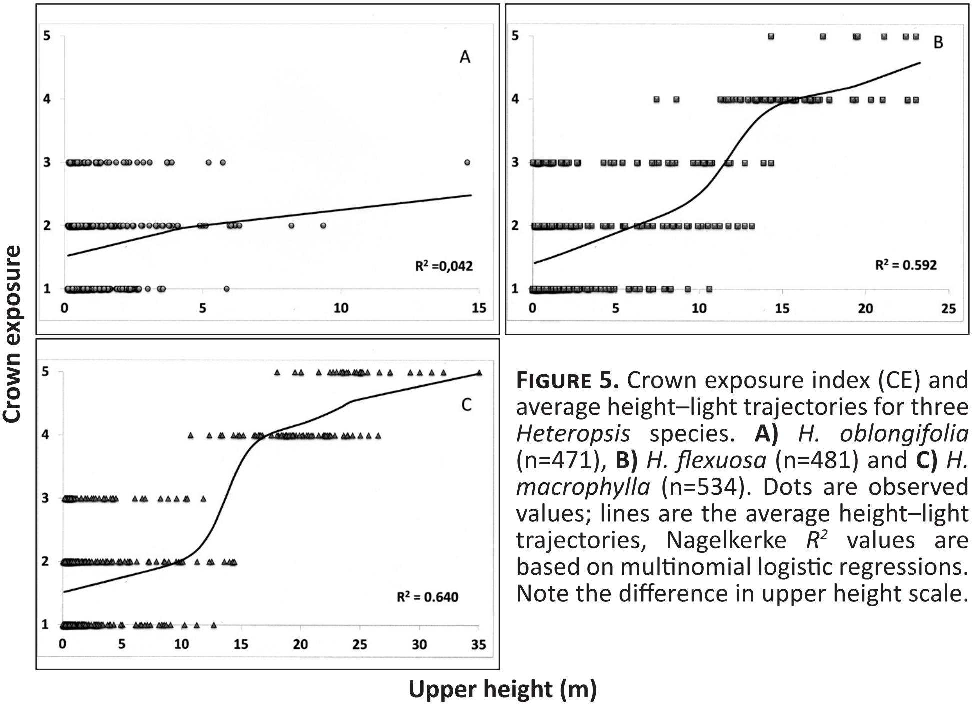

FIGURE 5. Crown exposure index (CE) and average height–light trajectories for three *Heteropsis* species. **A)** *H. oblongifolia* (n=471), **B)** *H. flexuosa* (n=481) and **C)** *H. macrophylla* (n=534). Dots are observed values; lines are the average height–light trajectories, Nagelkerke R^2 values are based on multinomial logistic regressions. Note the difference in upper height scale.

VITAL RATES

SURVIVAL

We found that the annual survival of non-climbing seedlings was very low. The annual survival rate for non-climbing seedlings of all three species pooled was 28 % (N=39;

H. macrophylla: 17 and *H. flexuosa*: 22; Fig. 1B). This value is in sharp contrast with that of climbing *Heteropsis* seedlings. Annual survival probability of small climbing seedlings (0.01-0.25) ranged from 85 % for *H. flexuosa* to 94 % for *H. oblongifolia*. This survival rate did not differ between suitable and non-suitable hosts for any of the studied species (Table 2). For *H. oblongifolia* and *H. flexuosa*, survival probability increased with the upper height (*H. oblongifolia*: $ß_{\text{Upper height}} = 0.917$, $P= 0.025$, $R^2=0.055$; *H. flexuosa*: $ß_{\text{Upper height}} = 0.532$, $P=0.001$, $R^2=0.167$; logistic regression), but not for *H. macrophylla* ($ß_{\text{Upper height}}$ = ns, $R^2=0.002$, logistic regression) (Fig. 6 A, B, C). It should be noted, however, that the explained variation of these logistic regressions is very low. The annual survival probability based on two years for fallen individuals varied between 68 % (*H. flexuosa*) and 78 % (*H. macrophylla*)

TABLE 2. Survival of the three *Heteropsis* species, using multiple logistic regressions. Significance: -= no tested; ns= $P \geq 0.05$; *= $P \leq 0.05$; **= $P \leq 0.01$; ***= $P \leq 0.001$. The maximum upper height included in this analysis was restricted to the maximum height of non-suitable hosts: *H. oblongifolia*: 0.01-1.5; *H. flexuosa*: 0.01-8.4 m; *H. macrophylla*: 0.01-6.0 m.

Species	***H. oblongifolia***	***H. flexuosa***	***H. macrophylla***
R^2	0.030	0.037	0.100
Constant	1.942***	1.702***	1.548***
Upper height	ns	0.320*	1.148*
Suitability	ns	ns	ns

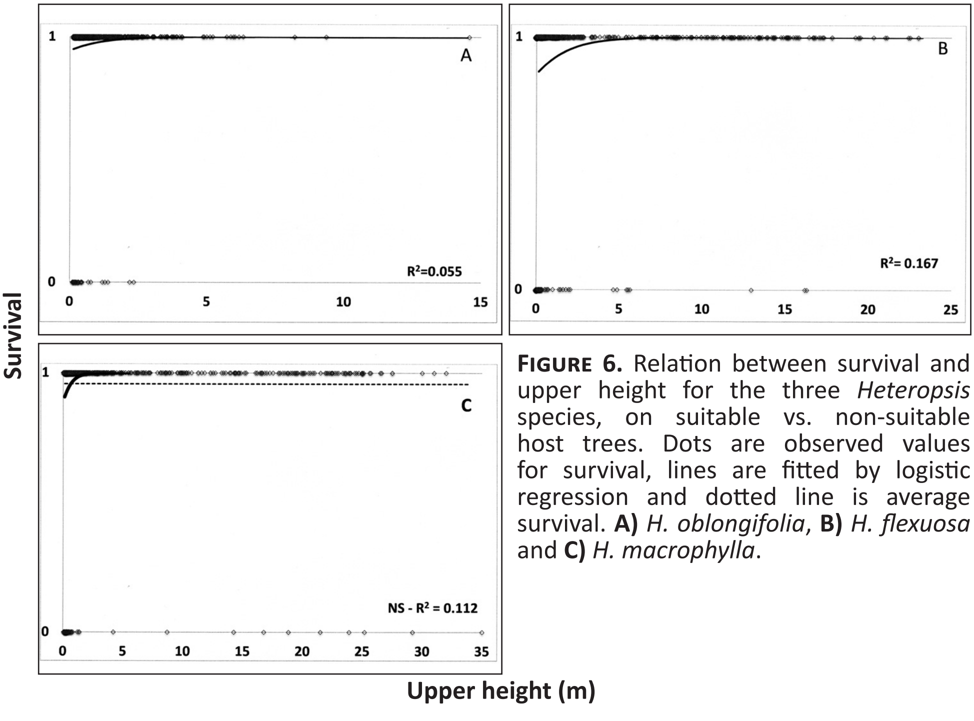

FIGURE 6. Relation between survival and upper height for the three *Heteropsis* species, on suitable vs. non-suitable host trees. Dots are observed values for survival, lines are fitted by logistic regression and dotted line is average survival. **A)** *H. oblongifolia*, **B)** *H. flexuosa* and **C)** *H. macrophylla*.

GROWTH

The three *Heteropsis* species showed slow and highly variable rates of height growth. In general, growth rate increased faintly with height (Fig. 7). Remarkably, 31 (*H. macrophylla*) to 62 % (*H. oblongifolia*) of the plants did not change in size at all or shrunk during two years. Average growth in upper height was 0.020, 0.076 and 0.079 m per yr-1 and maximum growth rate was 0.80, 2.78 and 2.93 m per yr-1 for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively. Since we were interested in understanding factors governing positive growth, we performed statistical tests on individuals with positive growth rates. Firstly, we did not find significant differences in positive growth rate between plants on non-suitable and suitable hosts (ANCOVA; effect of suitability: *H. oblongifolia*: $F_{1-115}=1.935$, $P=0.167$; *H. flexuosa*: $F_{1-180}=0.003$, $P=0.960$; *H. macrophylla*: $F_{1-255}=0.671$, $P=0.413$). Secondly, the positive upper height growth rate was positively related to initial upper height, crown exposure and number of absorbing roots in *H. macrophylla* (Table 3). In contrast, the positive growth rate did not vary with respect to crown exposure, but did so with the number of absorbing roots in the understory species *H. oblongifolia* (Table 3). These variables explained 27 to 49 % of the variation in positive upper height growth. So, individuals with more access to light and a higher number of absorbing roots grew faster.

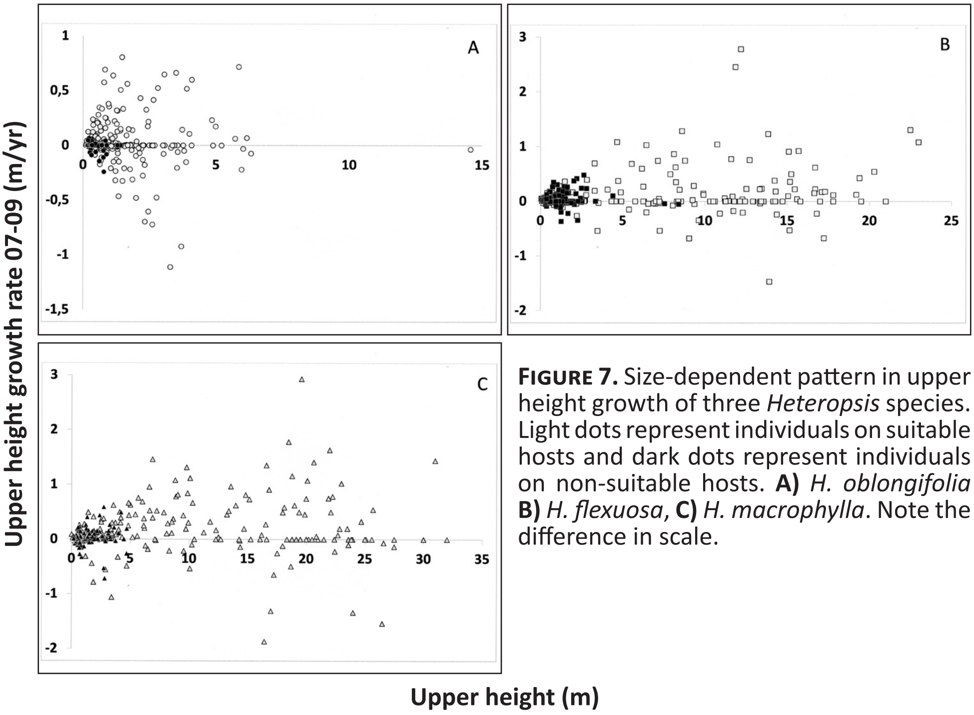

FIGURE 7. Size-dependent pattern in upper height growth of three *Heteropsis* species. Light dots represent individuals on suitable hosts and dark dots represent individuals on non-suitable hosts. **A)** *H. oblongifolia* **B)** *H. flexuosa*, **C)** *H. macrophylla*. Note the difference in scale.

Table 3. Natural log-transformed positive upper height growth rate in relation to upper height, crown index (CE) and number of absorbing roots of three *Heteropsis* species, using multiple linear regressions. Dummy variables were assigned to each crown index and categories for the number of absorbing roots. Significance: -= no tested; ns= $P \geq 0.05$; *= $P \leq 0.05$; **= $P \leq 0.01$; ***= $P \leq 0.001$.

Species	*H. oblongifolia*	*H. flexuosa*	*H. macrophylla*
R^2	0.277	0.268	0.490
Constant	-4.037***	-2.752***	-3.789***
Upper height	0.659***	0.099***	0.229***
CE2	ns	ns	ns
CE3	ns	0.853*	0.552**
CE4	-	ns	-1.622***
CE5	-	ns	-2.907***
2 absorbing roots	ns	ns	0.407**
3 absorbing roots	0.824*	ns	0.865***
≥4 absorbing roots	1.254*	ns	0.787***

SEXUAL REPRODUCTION

The three study species reproduced both sexually and asexually during the two observation years. The chance of being reproductive (i.e. presence of inflorescence) in *H. flexuosa* and *macrophylla* was strongly related to upper height and the number of plagiotropic branches. *H. oblongifolia*, however, showed a relation with the upper height but not with the number of branches. *H. flexuosa* and *macrophylla* produced inflorescences above 10 m upper height and *H. oblongifolia* above 1.5 m. Of these individuals, 33 and 51 percentage produced inflorescences for *H. macrophylla* and *flexuosa* respectively and 15 percent for *H. oblongifolia*. The relation of the upper height, plagiotropic branches and the reproductive status is shown in Fig. 8.

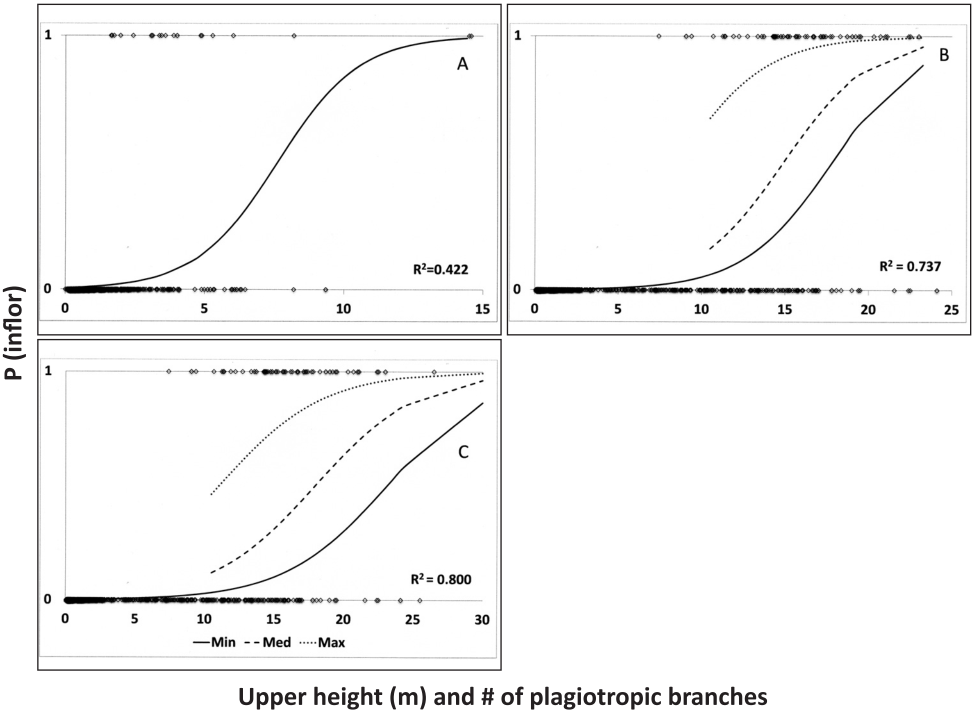

Figure 8. Relation between probability of inflorescence production (*P*(inflor)), the upper height and number of plagiotropic branches based on forward multiple logistic regressions. Dots are observed values for inflorescence production; lines are fitted by logistic regression. For *H. flexuosa* and *H. macrophylla*: The continuous line represents the minimum, the dashed the average and the dotted represent the maximum observed number of plagiotropic branches per height. **A)** *H. oblongifolia*: ß$_{\text{Upper height}}$ = 0.931, $P \leq 0.001$, ß$_{\text{plagiotropic branches}}$ = ns, $R^2=0.422$; **B)** *H. flexuosa*: ß$_{\text{Upper height}}$ = 0.376, $P \leq 0.001$, ß$_{\text{plagiotropic branches}}$ = 0.183, $P=0.01$, $R^2=0.737$; **C)** *H. macrophylla*: ß$_{\text{Upper height}}$ = 0.269, $P \leq 0.001$, ß$_{\text{plagiotropic branches}}$ = 0.232, $P=0.022$, $R^2=0.800$, multiple logistic regressions. Note the difference in scale in the upper height.

The number of the inflorescences produced per plant was not significantly related to the upper height for *H. flexuosa* and *oblongifolia* (*H. oblongifolia*: $F_{1\text{-}20}=1.064$, $R^2=0.106$, *P* upper height=0.173, *P* year=0.891; *H. flexuosa*: $F_{1\text{-}68}=0.910$, $R^2=0.027$, *P* upper height =0.383, *P* year=0.355; *H. macrophylla*: $F_{1\text{-}83}=14.486$, $R^2=0.1590$, *P* upper height =≤0.001, *P* year=0.752, multiple linear regressions). The maximum number of inflorescences per plant per year was 6, 16 and 22, but the average was just two, three and five inflorescences per plant per year for *H. oblongifolia*, *flexuosa* and *macrophylla*, respectively.

Vegetative Reproduction

The probability of segregating into two segments did not differ significantly between suitable and non-suitable hosts (*H. oblongifolia*: ß$_{\text{suitability}}$ = -0.791, *P*=0.277; *H. flexuosa*: ß$_{\text{suitability}}$ = -0.230, *P*=0.677; *H. macrophylla*: ß$_{\text{suitability}}$ = 0.263, *P*=0.570, multiple linear regression), but did increase with length for the three species (Table 4). *H. oblongifolia* was two times more likely to divide as the plant increased with length compared to the other two species (Table 4).

Table 4. Relationship between the probability of segregating into two and length in the three *Heteropsis* species using multiple logistic regressions. Significance: ns: *P* ≥0.05, *: *P*≤0.05, **: *P* ≤0.01, ***: *P* ≤0.001.

Species	***H. oblongifolia***	***H. flexuosa***	***H. macrophylla***
R^2	0.066	0.038	0.026
Constant	-4.790***	-3.781***	-3.684***
Length	0.528***	0.143***	0.089***

Heteropsis individuals on non-suitable hosts occasionally produced a flagellar shoot to the ground, which produced longer internodes and reduced their leaf size without changing its form. Once it reached the ground, it became a terrestrial stolon without leaves. Those stolons that found a new host generally lost their connection with the ortet after one of two years, thus becoming a ramet (Table 5). The probability that an individual produced a ramet that descended to the ground, and then climbed a host and split was significantly different between the type of host in *H. oblongifolia*, being higher in non-suitable host (ß$_{\text{Upper height}}$ = 1.588, *P*=0.009, ß$_{\text{suitability}}$ = -1.488, *P*=0.002, R^2=0.072, multiple logistic regression) and did not show significant differences between years (ß$_{\text{Upper height}}$ = 1.588, *P*=0.009, ß$_{\text{upper height}}$ and ß$_{\text{year}}$ = ns, R^2=0.011, multiple logistic regression). In *H. oblongifolia*, changing host through ramet production was significantly related to the upper height in non-suitable hosts (ß$_{\text{Upper height}}$ = 1.713, *P*=0.036, R^2=0.048, logistic regression), but not in suitable hosts (ß$_{\text{Upper height}}$ = ns, R^2=0.003, logistic regression). We could not statistically test whether there were differences in the probability of this type of vegetative reproduction between years and between the two types of hosts in *H. flexuosa* and *macrophylla*, due to the low number of observations. *H. flexuosa* and *macrophylla* had a low probability of vegetative propagation on non-suitable hosts, while almost no ramet production was found on suitable hosts (Table 5).

Table 5. Annual probability of ramet production and of connection loss with the ortet by the three *Heteropsis* species for individuals on non-suitable or suitable hosts. Observed probabilities are shown except for *H. oblongifolia* on non-suitable hosts, which gives a range based on a logistic regression with increasing probability with upper height.

Species	*H. oblongifolia*	*H. flexuosa*	*H. macrophylla*
Non-suitable	0.027 – 0.19	0.014	0.012
Suitable	0.016	0.003	0.0

The probability of falling (from or with the host) did not show differences between the types of host in *H. flexuosa* and *macrophylla* (*H. flexuosa*: $\chi2$=3.528, $P \geq 0.05$ ns *df*: 1 and *H. macrophylla*: $\chi2$=2.137, $P \geq 0.05$ ns, *df*: 1, Pearson Chi-square). In contrast, *H. oblongifolia* did differ between host types (*H. oblongifolia*: $\chi2$=28.023, P=0.000 *df*: 1, Pearson Chi-square). Due to the low number of observations we could not test whether the probability of falling was related to upper height. The annual chance of falling was 2 % for *H. flexuosa* and *macrophylla* and 7 and 0.9 % for *H. oblongifolia* on non-suitable and suitable hosts, respectively. After an individual fell, the non-absorbing roots should remain intact and attached to the forest floor; otherwise the plant had no chance of survival. If the plant survived, it produced shoots that eventually could climb a host, and might separate from the ortet in less than a year or two. This type of vegetative reproduction occurred in all three species. *H. oblongifolia* showed the highest (46 %, n=29), whilst *H. macrophylla* had the lowest probability of such vegetative propagation (15 %, n=7). The ramets of *H. flexuosa* and *macrophylla* climbed up to around 70 % (*H. flexuosa*: n=35; *H. macrophylla*: n=10) of the cases on non-suitable hosts, while *H. oblongifolia* scored only 43 % (n=53).

DISCUSSION

CHANGES IN PLANT SIZE AND ARCHITECTURE WITH HEIGHT

Secondary hemiepiphytes start their life on the dark forest floor, climbing up until they reach the understory (*H. oblongifolia*) or the (sub-)canopy (*H. flexuosa* and *macrophylla*). Once these plants ascend on a host, they begin to increase in height, increasing slowly in length, leaf size, number of roots and plagiotropic branches; raising also their chance of segregating with increasing length. Our (sub-)canopy species presented the highest number of absorbing roots and had the longest orthotropic stems as well. Hoffman (1997) and Plowden et al. (2003) reported the number of *H. flexuosa* roots in Guyana and Brazil, respectively, but their results are difficult to compare because they recorded the number of roots per host and not per individual plant.

The number of plagiotropic branches increased linearly and leaf size increased logarithmically with the upper height, but leaves never changed in form in the three species. The trend shown by our *Heteropsis* species is an example of allomorphic or ambiguous

heteroblasty (Ray 1992, Zotz, Wilhelm and Becker 2011), in which leaves change in size but not in form (Ray 1987, 1990, 1992). Lee & Richard (1991) also recorded that some hemiepiphytic Araceae increased their leaf size as they reached higher positions on their hosts.

FACTORS INFLUENCING SURVIVAL

The highest mortality (72 %) in our three *Heteropsis* species was found among non-climbing seedlings, caused by falling palm leaves, branches or other debris. This was also described for *Monstera* species (Ray 1976) and other plants in tropical forest understory conditions (cf. Clark & Clark 1989, Oyama 1990). Another cause of mortality was when the germinated seeds depleted their resources and the plants died without finding a host (Ray 1976). Non-climbing *Heteropsis* seedlings are still attached to their seeds and lack of leaves to photosynthesize, which makes them much more vulnerable to exhaustion of reserves and limit their ability to recover from damage. The mortality rate of non-climbing *Heteropsis* seedlings was much higher than that of free-standing (not yet climbing) liana seedlings, for which mortality rates of 14 – 17 % (<30 cm length, Nabe-Nielsen 2004) to 29 % (<50 cm tall, Gerwing 2004) were reported. The mortality probability of our *Heteropsis* species decreased dramatically once they climbed a host (6-15%), a phenomenon also observed among a secondary hemiepiphyte (*Monstera gigantea*) and lianas (Ray 1976, Nabe-Nielsen 2004, Gerwing 2004). Nonetheless, climbing *Heteropsis* seedlings have higher survival rates than shade-tolerant seedlings of other life forms smaller than 50 cm (Bierzychudek 1982, de Steven 1994, Zagt 1997, Zuidema & Boot 2002). *Heteropsis* as other secondary hemiepiphytes are appressed to the trunk; this may reduce damage and mortality from falling debris (Ray 1976). Thus, the very high mortality rate of non-climbing seedlings of secondary hemiepiphytes may constitute an important demographic bottleneck. Overcoming this high-mortality phase by quickly encountering a host therefore seems critical in the life history of these species.

Branch and tree-falls are frequent in tropical forests (van der Meer & Bongers 1996). In such a dynamic system, the longevity of the host might often limit the longevity of epiphytes more than any other (a-)biotic factor such as drought (Benzing 1990). Therefore, it is important that epiphytic plants can survive such events. Climbing *Heteropsis* individuals can survive after falling on the forest floor, with a remarkable survival probability (up to 78 %). This is substantially higher than survival rates of fallen epiphytes (Matelson et al. 1993), but comparable to survival values obtained for rattans (Putz 1990a) and lianas (90 %, Putz 1984). The survival of fallen lianas, their ability to reach the canopy again and to produce physiologically independent ramets, has been suggested to result in very long-lived genets (Nabe-Nielsen & Hall 2002). The high survival probabilities of climbing *Heteropsis* individuals together with their ability to produce ramets, suggest that these species may reach high ages.

Factors Governing Growth

Our study shows that the three *Heteropsis* species grow very slowly in height (0.020 - 0.079 m yr-1) with a substantial number of individuals (31 to 62 %) not growing at all or shrinking over a two-year period. These results contrast with Hoffman's (1997) findings on *H. flexuosa*, for which he reported a mean height growth rate of 0.114 m in a six-month period; although he also recorded that 48 % of the plants did not growth. These slow growth rates also contrast sharply with fast-climbing rattans and lianas (Bøgh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, 1990b, Schnitzer 2005). Growth rates reported for natural rattan populations varied from 0.15 to 1.42 m yr-1 (Binh 2009, Bøgh 1996). For lianas, height growth amounted to 0.078 m yr-1 for small individuals of *Machaerium cuspidatum* (Nabe-Nielsen 2002) and 0.15 and 0.94 m yr-1 for five species that were experimentally supported (Putz 1984). In contrast to what was expected, relative growth rates of our *Heteropsis* species were lower than those of self-supporting species. Height growth rates reported for shade-tolerant tree seedlings in Costa Rica were 10 to 25 times higher (Clark & Clark 2001).

We found size-dependent growth rates, with the lowest rates among seedlings and increasing rates among juveniles and adults as they grew higher up in their hosts. The median growth rates (0, 0.008, and 0.026 m yr-1, *H. oblongifolia*, *flexuosa* and *macrophylla* respectively) suggest that the mean was strongly affected by several rapidly growing orthotropic stems. The similar results of *H. flexuosa* and *macrophylla* versus *oblongifolia* are caused by the fact that, on average, (sub)-canopy hemiepiphytes grow much faster once they reach an altitude of 10 to 15 m on a host. Seedlings growth rates are quite similar between the three species.

Growth rates in upper height varied widely among individuals. There was a high incidence of negative growth, with up to 27 % of the plants experiencing shrinkage. This occurred when orthotropic branches fell off because of falling debris, as a result of herbivory, or when canopy animals detached them from the host. The variation in positive growth rates in *Heteropsis macrophylla* can be explained by crown exposure and number of absorbing roots and in *Heteropsis oblongifolia* by just the number of roots. The results of *H. macrophylla* are similar to those of the shade-tolerant lianas *Machaerium cuspidatum* and *Connarus turczaninowii* (Nabe-Nielsen 2002, Aide & Zimmerman 1990), and for another six rattan species (Binh 2009, Bøng 1996), where height growth rates increased with increasing light levels. Although upper height growth in *Heteropsis* is certainly light-limited, water limitation may play an additional role. This role of water limitation is suggested by the effect of the number of absorbing roots on height growth rate. New studies showed that as adult *Heteropsis* plants ascend in height on a host, increase both the number as the thickness of the absorbing roots, clearly increasing the hydraulic efficiency, which is defined as the amount of water that can pass through a certain structure (root, stem, petiole) per unit of time and pressure gradient (Martínez-Vilalta and Piñol 2003, Gil-Pelegrín et al. 2005, Burgess et al. 2006). In other words, as the roots increase their diameter, they are able to transport more water and therefore to sustain a bigger amount of biomass (Turriago pers. comm.).

High proportions of *Heteropsis* and tendrillate lianas seedlings climb up in non-suitable hosts where they cannot complete their life cycle (Putz 1984, Putz & Holbrook 1991, Nabe-Nielsen 2001, Sakai et al. 2002, Chapter 2). Because individuals growing on non-suitable hosts have limited vertical support and they tend to invest more resources in producing shoots that move downwards searching for new hosts; we expected that plants on suitable hosts would grow faster than those on non-suitable ones. However, no significant differences in the upper height growth rates between non-suitable and suitable host were found in any of the species. In contrast, lianas were found to grow two to seven times faster when suitable supports were experimentally provided (Putz 1984). The suitability of the host did not affect survival and growth in the short term of our three *Heteropsis* species.

REPRODUCTION AND VEGETATIVE REPRODUCTION

The three study species reproduced both sexually and asexually during the two years of observations. Like many other species, *Heteropsis* species must reach a threshold size before beginning to reproduce (Gross 1981, Klinkhamer et al. 1987, Ohlson 1988, Primack & Hall 1990, Méndez & Obeso 1993). The probability of inflorescence production for the canopy *Heteropsis* species increased with the upper height and the number of plagiotropic branches. Plants with the same upper height but with more branches might produce more inflorescences, because they are only produced on those branches. On the other hand, the number of the inflorescences produced per plant was not significantly related to upper height in two of the three species. Binh (2009) found that in rattans the number of inflorescences produced was size-related; size dependence in sexual reproduction also is the rule in palms (Svenning 2000).

The probability of segregating into two segments in our *Heteropsis* species did not differ significantly on the two host types, although the average and maximum length between the two differed considerably. Nonetheless, the probability of segregating did increase with the length in the three species, which may be caused by cavitation or embolism (Tyree & Sperry 1989).

As the majority of the *Heteropsis* seedlings climbed non-suitable hosts, these plants were obliged to search for a new host. Vegetative propagation allows *Heteropsis* to move from a non-suitable host to a suitable one (Chapter 2). The probability that an individual produced a ramet that descended to the ground, and then climbed a host and splits, was significantly different between the two host types (non-suitable vs. suitable) in *H. oblongifolia*. Changing host through ramet production was size-dependent on non-suitable hosts, but not on suitable hosts (see Fig 5, Chapter 2). On the contrary, the canopy species had a low probability of vegetative propagation on non-suitable hosts, while almost no clonation was found on suitable ones. This type of vegetative propagation was described for other aroids as well (Ray 1976, 1992, Andrade & Mayo 1998, 2000). In the three *Heteropsis* species, this behavior seems more a dispersion-propagation strategy

to find a suitable host than a growth strategy to increase the size of the genet (Ray 1976, Chapter 2).

When, a *Heteropsis* climbs a host or finally reaches the canopy its problems are not over; a *Heteropsis* suffers severally when its support falls. The probability of falling did not differ between host types for the two canopy species, whereas the understory species did present significant differences. This divergence might be attributed to the differences in the definition of host suitability between the canopy and understory species: where non-suitable hosts of *H. oblongifolia* are those ≤1.5 m and for *H. flexuosa* and *macrophylla* ≤9 m height. Seedlings and saplings ≤1.5 m run a higher risk of dying or being buried under branches or debris than small trees ≤9m (cf. Oyama 1990, Clark & Clark 1989, Zuidema & Boot 2002).

The three *Heteropsis* species showed sprouting after falling from or with a host, especially *H. oblongifolia* (probability of 46 %). Although fallen epiphytes may not die immediately, their chance of ever producing successful progeny is virtually zero (Hietz et al. 2002). Lianas, however, vigorously sprout after falling in natural and selectively logged forests (Putz 1984, Appanah & Putz 1984). The capacity to survive falls from the canopy confers a considerable advantage on lianas in that they attain a degree of immortality – at least in a biomechanical sense (Putz & Holbrook 1991). To sum up, vegetative propagation allows *Heteropsis* to survive hydraulic failure, and acts as a dispersion-propagation strategy to find a suitable host and reach the canopy again after falling.

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Drawing of a *Heteropsis flexuosa* seedling (Drawing by Maria Teresa Vargas-Paz).

Chapter 4

The significance of host suitability for the demography of secondary hemiepiphytes

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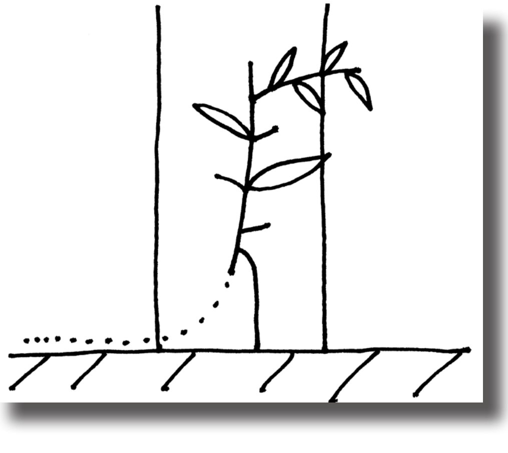
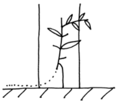
to be submitted





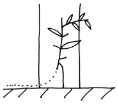
The significance of host suitability for the demography of secondary hemiepiphytes

ABSTRACT

Secondary hemiepiphytes in tropical forests start their life cycle at the forest floor and then climb into host trees to complete their life cycle. These species need tall host trees to become reproductive, yet most recruited seedlings climb on unsuitable hosts. Because such seedlings are able to switch hosts, they can still contribute to population growth. We wondered if plants on unsuitable hosts contribute to population growth. We studied demography of three *Heteropsis* species, in the Colombian Amazon. We distinguished *Heteropsis* sub-populations on suitable and non-suitable hosts and constructed multi-state matrix models to simulate population dynamics. Values of **λ** for all three *Heteropsis* species here studied were significantly ≥ 1, indicating that their populations are projected to grow. The mean age at reaching the reproductive size (τ) for *Heteropsis flexuosa* and *H. macrophylla* (10 m) was 58, while *H. oblongifolia* (1.5 m) was just 28 years. According to the elasticity values, population dynamics of the three species depend mainly on the large, adult individuals on suitable host. Elasticity and loop analyses showed that individuals on suitable hosts contributed much more to population growth, while those on non-suitable host were of negligible importance. Vital rates elasticity showed that survival on suitable hosts was more important than other vital rates for **λ**. Vegetative reproduction was more important to **λ** than sexual reproduction. We therefore conclude that the seedlings initially climbing onto non-suitable hosts can be considered as 'lost cases' for the population.

RESUMEN

Las hemiepífitas secundarias en los bosques tropicales comienzan su ciclo de vida en el suelo del bosque, posteriormente se trepan a árboles hospederos para completar su ciclo de vida. Estas especies necesitan hospederos altos para poder reproducirse, pero la mayoría de las plántulas reclutadas se suben a hospederos inadecuados (no lo suficientemente altos). Debido a que dichas plántulas son capaces de cambiar de hospedero, ellas todavía podrían contribuir al crecimiento de la población. Nos preguntamos si las plantas en hospederos inadecuados contribuyen al crecimiento de la población. Se estudió la demografía de tres especies de *Heteropsis*, en la Amazonia colombiana. Distinguimos sub-poblaciones de *Heteropsis* en hospederos adecuados e inadecuados y construimos matrices de población multi-estado para simular su dinámica de poblaciones. Los valores de **λ** para las tres especies estudiadas de *Heteropsis* fueron significativamente ≥ 1, lo que prevé que sus poblaciones están creciendo. La edad media a la cual alcanzan el tamaño reproductivo (τ) *Heteropsis*



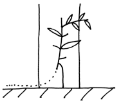
flexuosa y *H. macrophylla* (10 m) fue de 58, mientras que *H. oblongifolia* (1,5 m) fue de tan sólo 28 años. De acuerdo con los valores de elasticidad, la dinámica de las poblaciones de las tres especies depende principalmente de los adultos grandes en hospederos adecuados. Los análisis de elasticidad y del ciclo de vida mostraron que los individuos en hospederos adecuados contribuyen mucho más al crecimiento de la población, mientras que los individuos en hospederos no apropiados no tienen importancia. La elasticidad de las tasas vitales mostró que la supervivencia en hospederos adecuados es más importante que otras tasas vitales para λ. La reproducción vegetativa es más importante para λ que la reproducción sexual. Por consiguiente, concluimos que las plántulas que se trepan inicialmente a hospederos no adecuados, pueden ser consideradas como “casos perdidos” para la población.

Key words: *Amazon forest, Araceae, clonal or vegetative propagation, Colombia, elasticity analysis, Heteropsis, loop analysis, non-timber forest product, plant demography, matrix population models, source sink dynamics.*

INTRODUCTION

The life cycle of secondary hemiepiphytes involves two strongly contrasting life phases. In the first one, the host-searching phase, seeds germinate on the forest floor and search for a host. The second phase begins when the seedlings climb up a host and produce absorbing roots (Putz & Holbrook 1986, Plowden et al. 2003). Secondary hemiepiphytes belonging to the genus *Heteropsis* (Araceae) have seedlings that randomly “search” for vertical substrates or phorophytes (hosts, hereafter) to climb (Chapter 2). In contrast, seedlings of other hemiepiphytic species, such as *Monstera*, grow toward the darkness of a tree silhouette, a phenomenon known as skototropism (Strong & Ray 1975) or negative phototropism (Kaufman et al. 1989). The searching phase is brief (Chapter 2) but also rather risky, involving the highest mortality (72%) in the life cycle of secondary hemiepiphytes (Ray 1976, Chapter 2). In *Heteropsis* species, seedlings in this phase are leafless and growth is supported by relatively small seed reserves (M.P. Balcázar-Vargas, pers. obs).

The second phase in the life cycle of secondary hemiepiphytes begins when the seedling climbs a host and produces its first absorbing root growing downwards. When the roots reach the soil, the lower part of the stem dries out. To grow up, the plant produces vertical (orthotropic), and horizontal (plagiotropic) branches and more absorbing roots, and gradually sheds its lower parts (Putz & Holbrook 1986, Plowden et al. 2003). Sexual reproduction starts when individuals have reached a threshold size (Primack & Hall 1990, Mendez & Obeso 1993), which is correlated with the individual’s height on the host (Chapter 3). In a study on *Heteropsis’* hosts, we found that the vast majority of seedlings climbed onto non-suitable hosts (Chapter 2). Often, these individuals move to another host through vegetative propagation. Host-changing is a trial-and-error process that takes time (1-2 years; Chapter 2). Thus, it is likely that seedlings initially climbing suitable hosts contribute

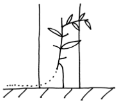


disproportionately to future reproduction and therefore to the population growth rate. However, since a large share of seedlings climbs onto non-suitable hosts, and these are able to move to suitable hosts, a part of the population on non-suitable hosts may also contribute to population growth in an indirect, delayed manner. Therefore, it is important to assess the relative significance of sub-populations on suitable and non-suitable hosts to population growth rate in order to determine the consequence of host-suitability for the demography of the secondary hemiepiphytes. For practical purposes here we use the term sub-populations, to define the set of plants that fell (fallen individuals) or were on non-suitable or suitable hosts. The survival and growth vital rates of the *Heteropsis flexuosa*, *H. macrophylla* and *H. oblongifolia* did not differ between suitable and non-suitable hosts (Chapter 3), but the impact of these vital rates to population growth may be quite different. To our knowledge, the demographic consequences of host suitability in hemiepiphytes or other climbing plants have not been studied so far.

Secondary hemiepiphytes on suitable and non-suitable hosts may be considered to be separate sub-populations with different functions. Individuals on suitable hosts act as a source sub-population since they produce offspring, while those on non-suitable hosts act as sink sub-populations because they would go “extinct” in the absence of reproduction coming from the source sub-population (suitable hosts). Consequently, when individuals move from non-suitable to suitable hosts, they shift from sink to source sub-populations. Theoretically, source sub-populations are able to maintain themselves via sexual reproduction, in contrast to sink sub-populations, which depend on input from source sub-populations (Hanski 1999). It has been shown that, if there is an excess of individuals produced by source sub-populations, the input in a sink sub-population can persist indefinitely (Pulliam 1988, Hanski 1999, Kawecki 2004).

The potentially harvestable aerial roots of *Heteropsis flexuosa* and *H. macrophylla* are confined to suitable hosts, because they belong to plants that have an upper height of 10 m or more. The roots preferred for craft production are the ones that drop straight to the ground, are mature, have the required pliability, thickness and length (Balcázar-Vargas & van Andel 2005). Aerial roots of these two species are used throughout the Amazon Basin to manufacture handicraft and cultural objects such as basketry as well as land and fish traps by indigenous people (Bennett 1992, Hoffman 1997, Balcázar-Vargas & van Andel 2005, Wallace, Pereira & Plowden 2011). These two species have become scarce around the indigenous communities due to intensive commercial exploitation (Balcázar-Vargas & van Andel 2005, Rodrigues-Ferreira & Bentes-Gama 2005, Wallace & Ferreira 2000). Hoffman (1997) estimated that *Heteropsis flexuosa* seedlings take 61 year to reach such a harvestable size threshold based only in 116 plants in a six month period. Analyses of the population dynamics of *Heteropsis* species on suitable and non-suitable hosts may provide more realistic and precise age estimates, which are relevant for their management.

We studied the ramet population dynamics of three *Heteropsis* species to address the following questions. (1) What is the relative contribution of *Heteropsis* individuals on suitable vs. non-suitable hosts for their population growth rates (**λ**)? We constructed multi-



state population matrix models (Caswell 2001), describing dynamics of *Heteropsis* subpopulations on non-suitable and suitable host (Horvitz & Schemske 1995, Zuidema et al. 2010) and carried out elasticity analysis (de Kroon et al. 1986, 2000, Caswell 2001) and loop analyses (Güneralp 2007) to evaluate the role of host types (non-suitable and suitable) on population growth rate. (2) What is the importance of various vital rates for $\boldsymbol{\lambda}$? In particular, we were interested in understanding the significance of vegetative reproduction as it enables individuals to move from non-suitable to suitable hosts. (3) What is the age at which *Heteropsis* species become reproductive, and at which their roots can begin to be harvested (due to their thickness)? To answer this question we used age-from-stage methods for population matrix models (Cochran & Ellner 1992, Caswell 2001, 2006).

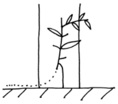
MATERIALS AND METHODS

STUDY SPECIES

Here we studied three species of the genus *Heteropsis* (Araceae). *Heteropsis flexuosa* (Kunth) G.S. Bunting, *H. macrophylla* A.C. Sm and *H. oblongifolia* Kunth are secondary hemiepiphytes distributed along the Amazon and much of Central America (for *H. oblongifolia*, Croat 1988). These species differ in their maximum height on hosts: 14 m for *H. oblongifolia* (understory), 25 m for *H. flexuosa* and 35 m for *H. macrophylla* ((sub)-canopy). They also differ in the height at which they become reproductive: *H. flexuosa* and *H. macrophylla* produce inflorescences at ≥ 10 m while *H. oblongifolia* at ≥ 1.5 m (Chapter 2).

STUDY SITE

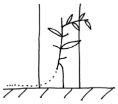
Field work was conducted at El Zafire Biological Research Station (ZBS) of the Universidad Nacional de Colombia, located in the southern-most part of the Colombian Amazon (4°0' S, 69°53' W, 80 m a.s.l. Fig. 3 in Chapter 1). The mean annual temperature of the region is 26 °C with a relative humidity of 86% (Jiménez 2007). The annual average precipitation is 3335 mm (data from the Vásquez Cobo airport of Leticia, Jimenez et al. 2009). The area is characterized by sandy soils and four major forest types: tierra firme, floodplain, white sand and transition forest (Peñuela & Alvarez 2006). All soil types contain old-growth evergreen forests with no evidence of human disturbance except for hunting. The field station is at least 12 km from the nearest indigenous communities, and no root harvesting has occurred at ZBS in the last decades (M. Balcázar-Vargas, pers. obs.). Specimens of all species were collected and identified at the Herbario Nacional Colombiano (COL).



SAMPLE DESIGN AND FIELD MEASUREMENTS ON *HETEROPSIS* PLANTS

To quantify the vital rates of survival, growth, falling, vegetative propagation and sexual reproduction in the three *Heteropsis* species, we conducted a study in three plots (0.7, 1 and 4 ha) in undisturbed tierra firme forest, two of which are permanent plots included in the RAINFOR network (Peñuela & Alvarez 2006), they are at least 1 km apart from each other. In 2007 we tagged and measured 758 individuals of *H. flexuosa*, 674 of *H. macrophylla* and 647 of *H. oblongifolia* in the aforementioned plots. For each *Heteropsis* individual, we measured its upper and lower height on the host employing a fiberglass telescopic rod or a measuring tape using climbing techniques (see Fig. 1, Chapter 3). The upper and lower heights of measurement were marked on the host with yellow permanent paint to facilitate tracking the next year. From a subset of the initial study population with upper height taller than 7, 8 and 1 m, for *H. flexuosa*, *H. macrophylla* and *H. oblongifolia*, respectively, we noted the reproductive status for 132, 93 and 109 individuals of *H. flexuosa*, *H. macrophylla* and *H. oblongifolia*, respectively, every month, during two years (2007-2009). In addition, we recorded the inflorescence and infrutescence production of these individuals. Furthermore, we also measured clonal propagation by recording and tagging branches of individuals that climbed onto other hosts. If during the next census we found that such a branch had lost connection with the parent plant (ortet, hereafter), we recorded this ramet as a new individual produced by clonal propagation. We categorized five types of vegetative reproduction that are common to all three species. Many of these result in a change of host (Chapter 2), but only the three most common were included in the demographic models employed in this study (Fig. 1, see Table 1 in Chapter 2). The type D (see Figure 5 and Table 1 in Chapter 2) occurs when a plagiotropic branch breaks down, falls and sends a ramet that eventually will climb a host. Type E occurs when a plagiotropic branch is in proximity of other host, it produces a flagellar shoot without touching the soil and climbs up the host next to it. These two types of cloning are really infrequent; they occur only around 0.20% per year (Chapter 2). The most common asexual reproduction types and included in this matrix are: the first occurs when the individual segregates in two parts (Fig. 1A), producing an ortet (the orthotropic branches below the split) and a ramet (the orthotropic branches above the split). The second type happens when a *Heteropsis* individual produces flagellar shoots to the ground, which eventually climb another host and split off (Fig. 1B); this type of ramet production has been already described for other Araceae species (Ray 1992; Andrade and Mayo 1998; 2000). The third type occurs when the individual falls (either along with its host or on its own) and then produces stolons that climb up new hosts, and eventually separate from the ortet (Fig. 1C). These forms of vegetative reproduction are referred to as *K1*, *K2* and *K3* below. Note that *K2* is the process that allows *Heteropsis* individuals on a non-suitable to move to another host (Fig 1B). To facilitate the measurements and the interpretation of branch and ramet production, we made drawings of all measured individuals every year. Fallen hosts or fallen hemiepiphytes were recorded.

The measurements were repeated in June – September 2008 and 2009, when survival and growth of the ortet and ramets, ramet production, fallen hosts or fallen hemiepiphytes and recruitment of the seedlings were recorded. Recruited seedlings of *H.*



flexuosa were searched, tagged and measured within 42 subplots of 10 x 10 m (0.42 ha) and for *H. macrophylla* and *H. oblongifolia* in 82 subplots of 10 x 10 m (0.82 ha) in the three plots.

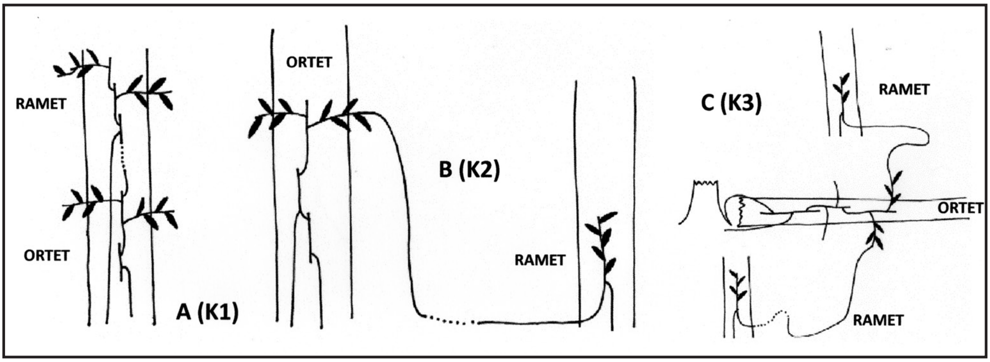
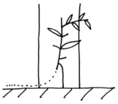


FIGURE 1. Cloning types: **A)** an orthotropic branch dies off (dotted line) and the plant survives in two parts (*K1*). **B)** A plagiotropic branch becomes a flagellar shoot, which climbs up a new host. After the climber has produced a new anchoring root, the ramet separates from the ortet (*K2*). **C)** The individual falls, with or without the host. A plagiotropic branch produces a stolon that climbs up new hosts, and eventually separates (*K3*). (Drawing by M.P. Balcázar-Vargas).

HOST MEASUREMENTS

In order to evaluate the role of host types, for each *Heteropsis* host the following variables were recorded: (1) dbh (for hosts with a height < 1.3 m, the stem diameter was recorded at half the trunk height); (2) total height and the height of its first branch; (3) whether the host was dead or alive, upright or fallen, and (4) its inclination. We did not specifically record information on bark characteristics of host, but we did not find any *Heteropsis* individual on a tree with a peeling bark and just one small seedling of *Heteropsis macrophylla* on a tree species which loses its bark as dust, (Mimosaceae). In this particular case, we classified this host as non-suitable. We categorized a host as non-suitable or suitable, based on the minimum height at which the three *Heteropsis* species reproduce (Chapter 2). A suitable host for *H. oblongifolia* was defined as alive, taller than 1.5m and with an inclination < 45°. The criteria of suitability were the same for *H. flexuosa* and *H. macrophylla*, but with a minimum height of 10 m. non-suitable hosts for the three species included small palms like *Lepidocaryum tenue* Mart., herbs like Marantaceae and Heliconiaceae, tree seedlings, tree ferns, and dead plants.



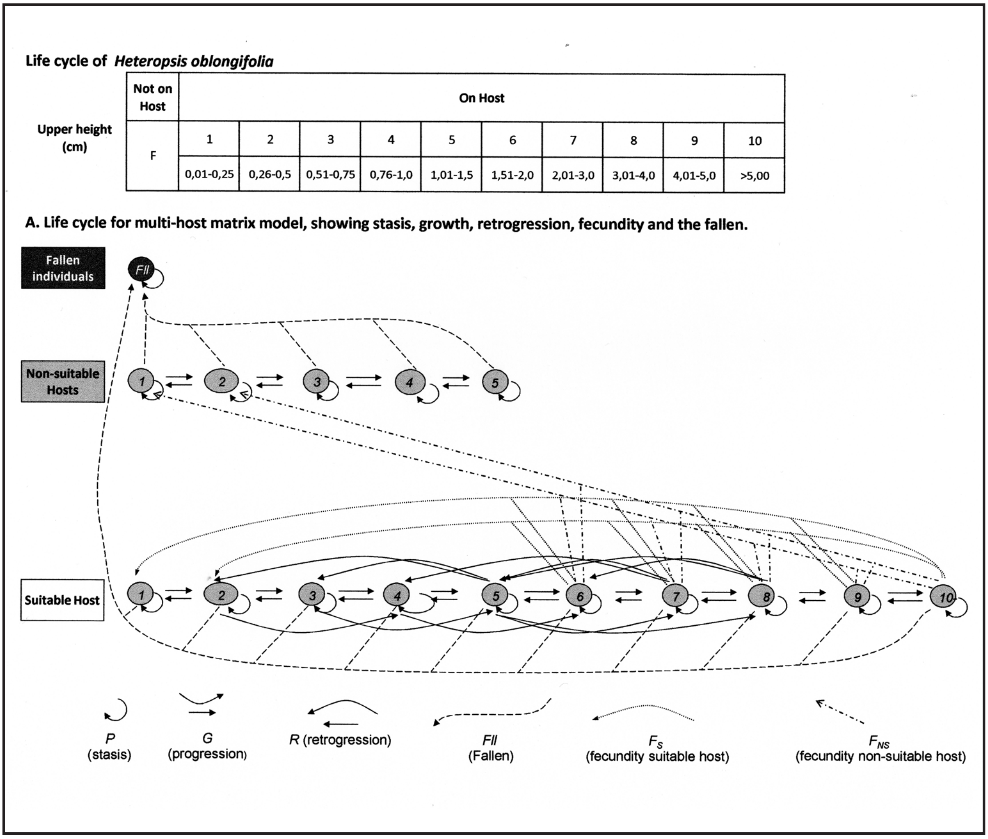
POPULATION MATRIX MODEL CONSTRUCTION

We used multi-state matrix models (Pascarella & Horvitz 1998; Caswell 2001; Zuidema et al. 2010) to model the population dynamics of the three *Heteropsis* species based on the three main states fallen individuals, and individuals on non-suitable and suitable hosts. The resulting transition matrices had 16, 39 and 41 categories for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively, corresponding to a combination of sub-populations (fallen plants, non-suitable and suitable) and individual sizes. We categorized individuals by size based on the upper height on their host (suitable or non-suitable). Our population matrices contain annual transitions based on dynamics observed during two years (2007–2009). Below, we explain the construction of a transition matrix for *Heteropsis oblongifolia* (for the other two species and for more details, see Appendix 2A, B & C and 3A, B & C). The resulting population matrix contains in total nine submatrices (**A**, **B**, **C**, **D**, **E**, **F**, **G**, **H** and **I**) (Table 1). The submatrices $\mathbf{A}_{1x1}$, $\mathbf{E}_{5x5}$ and $\mathbf{I}_{10x10}$, where the subindex indicates the dimension (i.e. number of stages), describe the dynamics within the fallen plants (submatrix **A**), non-suitable host (submatrix **E**) and suitable host (submatrix **I**). The other six submatrices (**B**, **C**, **D**, **F**, **G** and **H**) quantify the probability that a plant falls from a non-suitable or from a suitable hosts (**B** and **C**, respectively), the ramet production of fallen plants that climb non-suitable or suitable hosts (**D** and **G**, respectively), recruitment subsidies on non-suitable hosts and the ramet production from suitable to non-suitable hosts (**F**), and the ramet production from non-suitable to suitable hosts (**H**) (Table 1, Fig 2).

TABLE 1. Multi-state matrix of *Heteropsis oblongifolia*, *H. flexuosa* and *H. macrophylla*.

Matrix *Heteropsis*			**Class at t**		
			Not on Host	**On Host**	
			Fallen individuals	**Non-Suitable Host**	**Suitable Host**
Class at t+1	Not on Host	Fallen individuals	$\mathbf{A}_{1x1}$	$\mathbf{B}_{mx1}$	$\mathbf{C}_{nx1}$
	On Host	Non-Suitable Hosts	$\mathbf{D}_{1xm}$	$\mathbf{E}_{mxm}$	$\mathbf{F}_{nxm}$
		Suitable Hosts	$\mathbf{G}_{1xn}$	$\mathbf{H}_{mxn}$	$\mathbf{I}_{nxn}$

m (number of non-suitable stages) and ***n*** (number of suitable stages). *H. oblongifolia*: ***m***= 5 and ***n***=10; *H. flexuosa*: ***m***= 13 and ***n***=25; *H. macrophylla*: ***m***= 10 and ***n***=30.

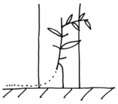


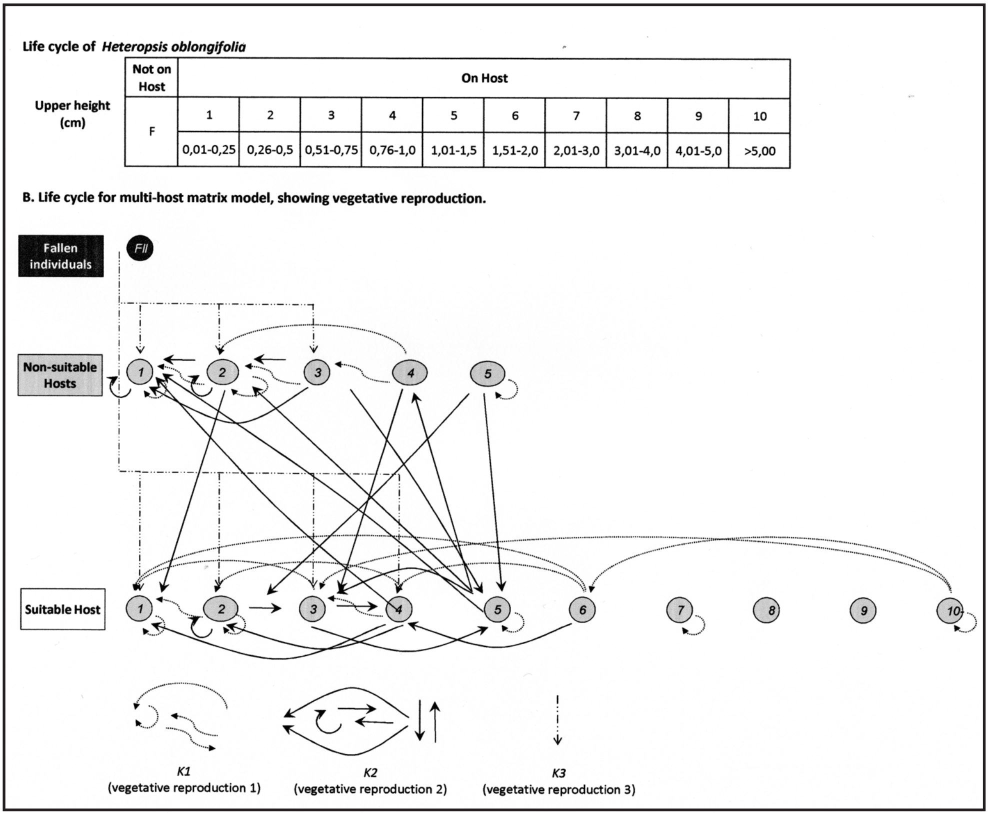
Life cycle of *Heteropsis oblongifolia*

	Not on Host	On Host									
Upper height (cm)	F	1	2	3	4	5	6	7	8	9	10
		0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	>5,00

A. Life cycle for multi-host matrix model, showing stasis, growth, retrogression, fecundity and the fallen.

FIGURE 2 A. Life cycle diagram for population matrix models of *Heteropsis oblongifolia*. Circles represent the life stages, based by sub-population type (fallen plants, non-suitable and suitable) and individual's size. To facilitate the visualization of the vital rates, we show the life cycle twice. Arrows indicate *P* (stasis), *G* (growth), *R* (retrogression), *Fll* (probability of falling), *Fs* (fecundity from suitable to suitable host) and *Fns* (fecundity from suitable to non-suitable host)





Life cycle of *Heteropsis oblongifolia*

	Not on Host	On Host									
Upper height (cm)	F	1	2	3	4	5	6	7	8	9	10
		0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	>5,00

B. Life cycle for multi-host matrix model, showing vegetative reproduction.

FIGURE 2 B. Life cycle diagram for population matrix models of *Heteropsis oblongifolia*. Circles represent the life stages, based by sub-population type (fallen plants, plants on non-suitable and suitable host) and individual's size. To facilitate the visualization of the vital rates, we show the life cycle twice. Arrows indicate *K1*, *K2* and *K3* (the most important types of ramet production – see Fig. 1). Life cycles of *H. flexuosa* and *macrophylla* were similar but contained 39 and 41 stages, respectively (Appendix 3B & C).

Elements a_{ij} in submatrices **A**, **E** and **I** can be grouped into stasis (P_{ij} for $i = j$), progression or growth (G_{ij} for $i > j$), retrogression or shrinkage (R_{ij} for $i < j$), two types of vegetative reproduction: ($K1_{ij}$; for $i = j$, $i < j$), segregating in two parts on the same host; ($K2_{ij}$ for $i = 1$ to 5 and $j = 1$ to 6), segregating in two parts on different hosts and recruitment into stage 1 (0.01-0.25 cm upper height) and stage 2 (0.26-0.50 cm upper height) on suitable hosts (F_{ij}; for $i = 1$ and 2 recruitment categories and $j > 6$ adult categories). Elements a_{ij} in submatrices **B**, **C**, **D**, **F**, **G**, **H** can be grouped into two types of vegetative reproduction ($K2_{ij}$ and $K3_{ij}$; for $i = 1$ and $j = 1 – 4$, fallen plant produced shoots that eventually climb a non-suitable or suitable host and separate), recruitment into stage 1 (0.01-0.25 cm upper height) and 2 (0.26-0.50 cm upper height) on non-suitable hosts (F_{ij}; for $i = 1$ and $j > 6$) and probability of falling (Fll_{ij} = for $i \geq 2$ to $j = 1$) (Table 2). Their values were calculated from the underlying vital rates. The relation between matrix elements and vital rates are shown in the Table 3.

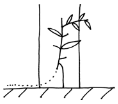
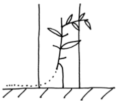


TABLE 2. Parameters and equations to calculate transition probabilities for three *Heteropsis* species. See Appendix 3 (booklet).

Matrix elements	Formula	
Stasis	$P_j = \sigma_j\ (1 - \sum_i \gamma_{ij} - \sum_i \rho_{ij})$	(1)
Progression	$G_{ij} = \sigma_j \times \gamma_{ij}$	(2)
Retrogression	$R_{ij} = \sigma_j \times \rho_{ij}$	(3)
Fecundity	$F_{ij} = \sigma_j \times \mathrm{Prob}\{f\}_j \times f_j$	(4)
Vegetative reproduction	$K1_{ij} = \sigma_j \times \kappa 1_{ij}$	(5)
	$K2_{ij} = \sigma_j \times \kappa 2_{ij} \times \mathrm{Prob}\{change\ host\ type\} \times \#\ ramets/\#\ ortet \times \mathrm{Prob}\{reach\ Stage\ 1\ to\ 4\}$	(6)
	$K3_{ij} = \sigma_j \times \kappa 3_{ij} \times \mathrm{Prob}\{type\ of\ host\} \times \#ramets/\#\ ortet \times \mathrm{Prob}\{reach\ Stage\ 1\ to\ 5\}$	(7)
Falling from a non-suitable host	$Fll_{ij} = \sigma_j\ x\ \pi ns_{ij}$	(8)
Falling from a suitable host	$Fll_{ij} = \sigma_j\ x\ \pi s_{ij}$	(9)

TABLE 3. Vital rates of *Heteropsis oblongifolia* as an example of the three species. All rates and probability are per year (yr-1).

Vital rates	Definition	Symbol
Survival	survival probability	(σ_j)
Growth	observed probabilities of growing from state *i* to stage *j*	(γ_{ij})
Retrogression	observed probabilities of shrinkage from state *j* to stage *i*	(ρ_{ij})
Vegetative reproduction 1	probability of segregating in two parts on the same host	$(\kappa 1_{ij})$
Vegetative reproduction 2	probability that an individual produced a ramet that descended to the ground and then climbed a host and split off	$(\kappa 2_{ij})$
Probability to change host	probability that a ramet produced on a non-suitable climbed another non-suitable host or a ramet produced on a suitable to climbed another suitable, or non-suitable to suitable or suitable to non-suitable	(Prob {change host-type})
Number of ramets produced per ortet	the number of ramets produced per ortet	(# ramets/ # ortet)

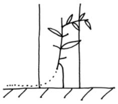


Vital rates	Definition	Symbol
Probability to reach a certain stage	probability that a ramet reached the first to fourth stages in upper height and splits off	(Prob{reach Stage 1 to 4})
Vegetative reproduction 3	probability that a fallen plant produced shoots that eventually climb a non-suitable or suitable host and split off	($\kappa 3_{ij}$)
Probability to climb a host	probability that a ramet climbs up on non-suitable or suitable host	(Prob{type of host})
Probability to be reproductive	probability that an individual in stage *i* (> 1.51-2.0 m) is reproductive	(Prob{f}$_i$)
Number of offspring	number of offspring produced by a reproductive individual in stage *i* (0.01-0.25 and 0.26-0.50 m upper height on suitable or non-suitable) host	($f_i ns$ or $f_i s$)
Probability of falling from non-suitable or suitable host	observed probabilities of falling from state *i* to stage 1	(πns_{ij} or πs_{ij})

MATRIX ANALYSES

For each species' matrix, we calculated the main set of population-level parameters that characterize their demographic dynamics. The main goal was to evaluate the relative contribution of *Heteropsis* individuals on suitable vs. non-suitable hosts for their population growth rates. Population dynamics were simulated as $\mathbf{n}(t + 1) = \mathbf{M}*\mathbf{n}(t)$ (Caswell 2001), in which **n** is a vector containing the population structure and **M** is the matrix containing all the possible transitions and a/sexual contributions between the stages (Fig. 2). We calculated the asymptotic population growth rate ($\boldsymbol{\lambda}$), the stable-stage distribution (**w**), and stage-specific reproductive values (**v**) for each *Heteropsis* species. We calculated the 95% confidence interval of the population growth rate with a parametric bootstrap resampling (n=9999) the projection matrix using a multinomial distribution for transitions and a log normal distribution for fertilities (Caswell 2001, Hall & Kaye 2001).

To determine if the values of the population growth are representative over a short period of time, the observed stage distribution (OSD) should be very similar to the predicted values of the stable stage distributions (SSD). Therefore we examine whether stable stage distributions were significantly different from the observed stage distribution. First, we normalized each vector to add up to one, and then used a Chi-square comparing observed and expected distributions for each of the three species. Then, we determined how far the OSD was from the SSD by calculating the proportional similarity index (PS sensu Horvitz & Schemske 1995) as:

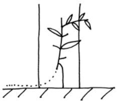


$$PS = \sum_{n}^{i=1} \min (ai,bi)\; x\; 100$$

where n are the stages in the lifecycle of the species of interest, ai and bi are the proportion of individuals in the i^{th} stage of the SSD and OSD, respectively. High values of PS indicate high similarity between both distributions.

The vast majority of *Heteropsis* seedlings climb up very small and non-suitable hosts and just a minority on suitable hosts (19%). As a consequence, those individuals cannot complete their life cycle because the reproduction of *Heteropsis* species is height dependent (Chapter 2 and 3). To evaluate the role of host types (non-suitable and suitable) on population growth rate we performed elasticity and loop analyses. The elasticity analysis quantifies the proportional effect of an infinitesimally small change in any of the elements or group of elements of the matrix on the population growth rate $\boldsymbol{\lambda}$ (de Kroon et al. 1986, 2000, Caswell 2001). We summed the values of the resulting elasticity matrix according to the three main states, fallen plants, non-suitable and suitable hosts, pulling all size classes, in order to quantify their relative contributions to $\boldsymbol{\lambda}$. In addition, we carried out the loop analysis to determine the contribution of pathways including the ‘fallen’ category, non-suitable hosts and suitable hosts to $\boldsymbol{\lambda}$. This analysis was introduced to demographic analysis as a tool to compare relative contributions of different life-history types to $\boldsymbol{\lambda}$ (van Groenendael et al. 1994). Loops are pathways through the life cycle with the same starting and ending stage. Loop analyses can be easily conducted for species with simple life cycles, as then the unique elements that are required for each loop can be readily identified (van Groenendael et al. 1994). However, the three study species have a complex life cycle and therefore loops cannot be readily defined. Therefore, we applied the approach of Güneralp (2007) that allows to calculate loop elasticity for complex life cycles. To calculate the loop elasticity of *Heteropsis* plants, the loop elasticity value was divided into the number of states (fallen, non-suitable and suitable) present in to the loop. As an example: a loop containing only fallen and non-suitable states, the loop elasticity value was divided into 2 and sum up to the total loop elasticity of the state.

Elasticity analysis has been widely used, but it contains a weakness in that the value of a matrix element is a function of more than one vital rate (Appendix 4 and Table 2). For example, transitions representing progression to larger size classes involve a survival rate as well as a growth rate. Ideally, then, demographic comparisons between populations should be made using elasticities of vital rates themselves, rather than elasticities of matrix elements that are compounds of those rates (Franco & Silvertown 2004). Unlike the elasticity of matrix elements, the elasticity of the underlying vital rates effectively separates the independent influence of the demographic processes on population growth (Franco & Silverstone 2004). Here, we conducted elasticity analyses on underlying vital rates (survival (σ_{ij}), growth (γ_{ij}), shrinkage (ρ_{ij}), falling (π_{ij}), sexual (f_{ij}) and three different types of asexual reproduction ($k1_{ij}$, $k2_{ij}$ and $k3_{ij}$) to determine their relative importance to $\boldsymbol{\lambda}$ (de Kroon et al. 1986, Caswell 2001). Because we are interested in measuring the magnitude of the change



and not its sign, throughout the paper we use the absolute value of elasticity of the vital rates. Finally, it should be noticed that the vital rate elasticities do not sum to 1 but to 2 (de Kroon et al. 1986, Caswell 2001). We applied formula for calculating vital rate elasticities published elsewhere (Franco & Silvertown 2004, Jongejans 2004).

We also analyzed the demographic significance of the non-suitable and suitable hosts using source-sinks dynamics (Diffendorfe 1998, Pulliam 1988, Hanski 1999). To determine whether non-suitable hosts are the sink populations we undertook an extreme perturbation analyses approach whereby we set all values in the sub-matrices **C**, **F**, **G**, **H** and I to zero and re-calculated $\boldsymbol{\lambda}$. To check whether the sub-population on suitable hosts is the source we set to zero the sub-matrices **B**, **D**, **E**, **F** and **H** to zero and again calculated $\boldsymbol{\lambda}$. As an example, If the sub-population on non-suitable obtain $\boldsymbol{\lambda}$ values <1, this sub-population is a sink. Meaning that the non-suitable population would go “extinct” in the absence of reproduction coming from the source sub-population (suitable hosts).

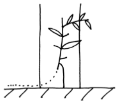
To determine the importance of the three type of vegetative reproduction, we also analyzed the demographic significance of ramet production by setting *K1* (probability of segregating in two parts on the same host), *K2* (probability that an individual produced a ramet that descended to the ground and then climbed a host and split off) and *K3* (probability of a fallen plant producing shoots that eventually climbed a non-suitable or suitable host and split off) to zero in the matrices and calculating the 95% confidence interval of the population growth rate with a parametric bootstrap resampling (n=9999) (Caswell 2001, Hall & Kaye 2001, Figure 1, Table 2).

In order to determine what is the age at which *Heteropsis* species become reproductive, and at which their roots can be harvested. We calculated the mean age at entering a category (τ) for the first reproductive category on suitable hosts (*H. oblongifolia*= 1.5-2.0 m; *H. flexuosa* and *H. macrophylla* = 10 -11 m on a host), using an equation that has been developed for matrix models in which individuals are grouped by size (Cochran & Ellner 1992, Caswell 2001). All analyses, except the loop analyses, were performed in R 2.14.1 (packages popbio, fBasics, Matrix and MASS); loop analyses were performed in Matlab 7.12.0 (MathWorks R2011a).

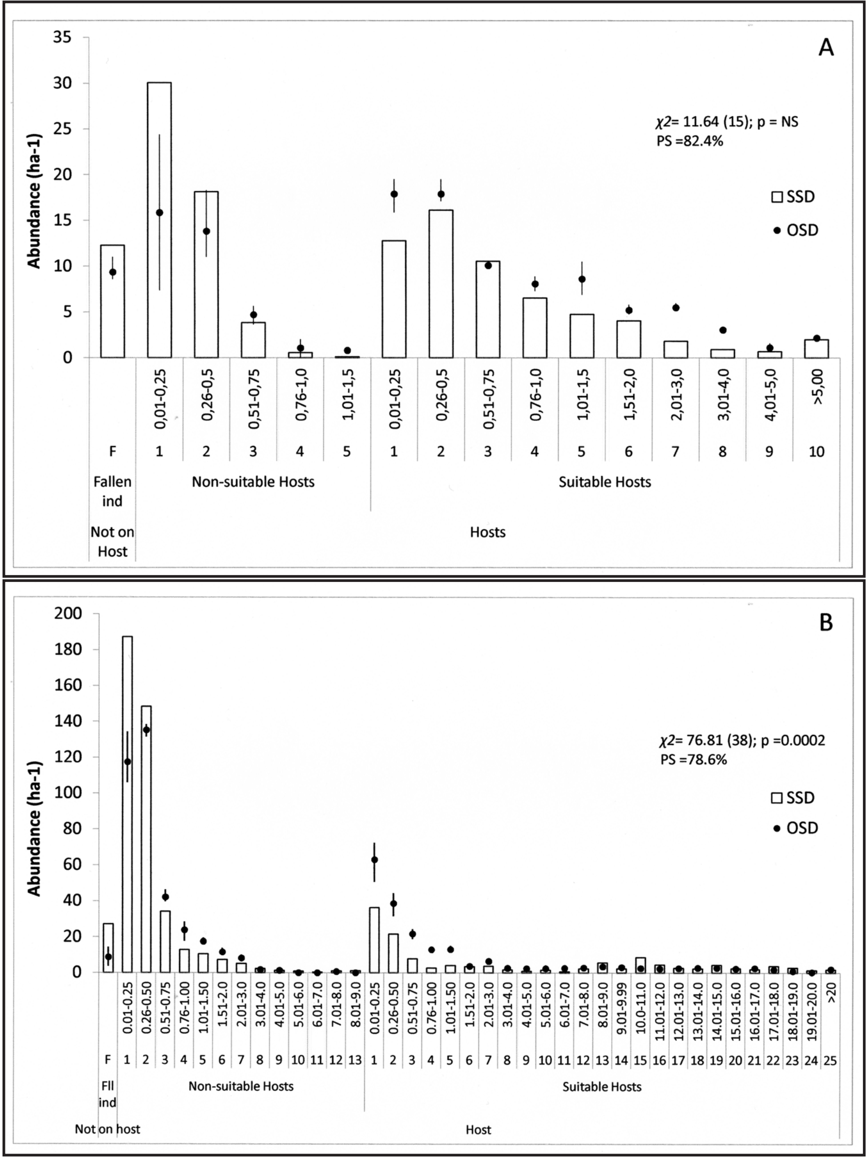
RESULTS

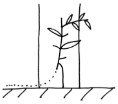
POPULATION STRUCTURES

The three *Heteropsis* species population structures (observed stage distribution, OSD) showed a declining abundance from small seedlings to large adult (Figure 1). Most of the individuals (36-62%) in the studied populations were present in the two smallest categories (0.01-0.25 and 0.26-0.5 m in height on non-suitable and suitable hosts; Fig. 3A, B, C). *H. flexuosa* and *H. macrophylla* had 2-7 individuals more climbing in the two first categories of non-suitable hosts than in the same categories of suitable hosts. In contrast, *H.*



oblongifolia had almost the same number of individuals in the two first categories in both types of hosts. The number of individuals per ha on non-suitable hosts were twice higher than on suitable hosts for *H. flexuosa* and *H. macrophylla*. The reverse trend was found for *H. oblongifolia*, with three times more individuals on suitable than on non-suitable hosts. Furthermore, the number of individuals on a host (non-suitable and suitable) per ha was much higher for *H. flexuosa* (560) that for *H. macrophylla* (99) and *H. oblongifolia* (116). *H. flexuosa* and *H. macrophylla* are two useful species, economically important across the Amazon. These two species have about 23 and 2 individuals per hectare, respectively.





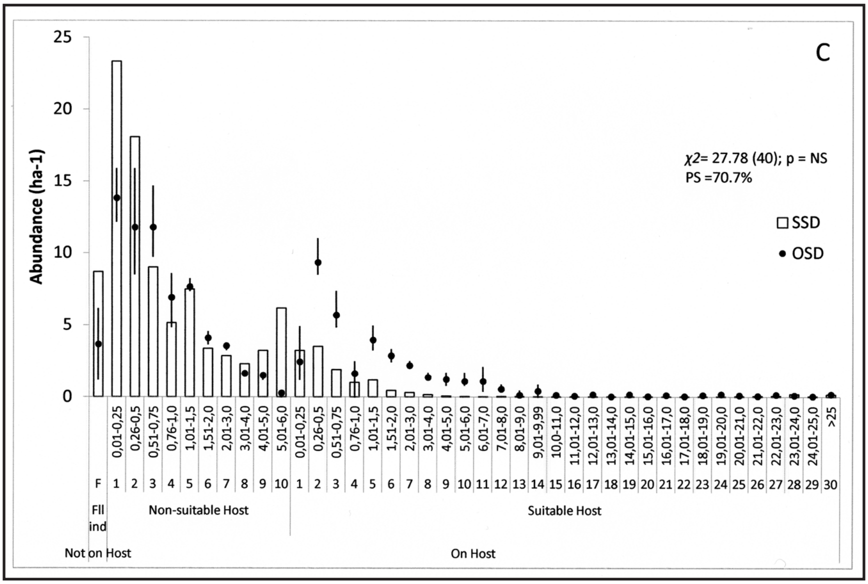
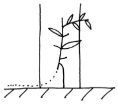


Figure 3. Stage distributions of three *Heteropsis* species. **A)** *H. oblongifolia*; **B)** *H. flexuosa*; and **C)** *H. macrophylla*. Dots (and thin lines on them) represent the mean (±SD) observed stage distribution (OSD) values between 2007 and 2009. Hollow bars are stable stage distributions (SSD) resulting from matrix models. The χ^2 statistic indicates whether there is a significant difference between the OSD and the SSD and PS indicates the magnitude of the difference between the two distributions.

POPULATION GROWTH

Asymptotic population growth rates (**λ**) and the 95% bootstrap confidence interval were ≥ 1 for all species during the observed period: 1.0446 (95% CI 1.0025- 1.1230) for *H. oblongifolia*, 1.0379 (1.0000- 1.2069) for *H. flexuosa* and 1.0101 (1.0000- 1.1002) for *H. macrophylla*. The seedling stages had the smallest reproductive values (less than 1% per stage). The reproductive value increased in general with size class from juveniles to adults, as these stages had lower mortality and as fertility also increased with size. The highest reproductive values were found among the tallest individuals.

To determine if the values of the population growth are representative over a short period of time, we establish the differences between the OSD and SSD. The OSD of *H. flexuosa* differed significantly from the expected stable-stage distribution (SSD; Chi-square: *H. oblongifolia*: χ^2=11.64, *df*: 15, *P*=0.7060; *H. flexuosa*: χ^2=76.81, *df*: 38, *P*=0.0002 and *H. macrophylla*: χ^2=27.78, *df*: 40, *P*= 0.9279; Fig. 3B). Nevertheless, the proportional similarities (PS) of *H. flexuosa* indicated rather close resemblance between the OSD and the SSD (*H. oblongifolia*: x=82.48, SD=0.046, N: 16; *H. flexuosa*: x=78.68, SD=0.050, N: 39 and *H. macrophylla*: x=70.71, SD= 0.032, N: 41).



The Role Of Host Suitability

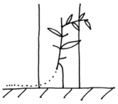
Seedlings initially climbing onto suitable hosts may contribute disproportionately to future reproduction and therefore to the population growth rate, due to the vast majority of seedlings climbed onto non-suitable hosts (Chapter 2). Here we assessed the relative significance of plants on suitable and non-suitable hosts to population growth rate in order to determine the consequence of host-suitability for the demography of the secondary hemiepiphytes. We use three different approaches: source sink dynamics, elasticity and loop analyses.

Source And Sink Dynamics

We analyzed the demographic significance of the non-suitable and suitable hosts by setting values in corresponding parts of the transition matrix to 0. Our results indicate that the sub-populations on suitable hosts are indeed sources in all three study species. In the absence of migration, understood as the production of ramets from suitable to non-suitable hosts and the production of seedlings that eventually climb non-suitable hosts, these sub-populations maintain $\boldsymbol{\lambda} > 1$, with $\boldsymbol{\lambda} = 1.0321$, 1.0372 and 1.0095 for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively. In contrast, the sub-population on non-suitable hosts (**E**) were found to be sinks as, in the absence of migration (i.e. the production of ramets from non-suitable to suitable hosts), they resulted in $\boldsymbol{\lambda} < 1$, with values of 0.9667, 0.9794 and 0.9892 for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively. These findings suggest that in absence of sexual reproduction the non-suitable sub-populations (sinks) will go locally extinct.

Elasticity Analysis

A comparison of the elasticity values of fallen plants, *Heteropsis* on non-suitable and suitable hosts showed highly similar results for the three species. *Heteropsis* plants on suitable hosts had the highest elasticity values with 85.6, 99.2 and 97.5%, whereas the plants on non-suitable hosts presented the lowest values with 10.1, 0.5 and 2.1% for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively (Appendix 4A, B, C). This result indicates that *Heteropsis* individuals on suitable hosts were of high importance for the population growth rate and maintenance of the populations of the three species, while non-suitable hosts had very low to hardly any importance for the population growth rates of the three species (Figure 4).



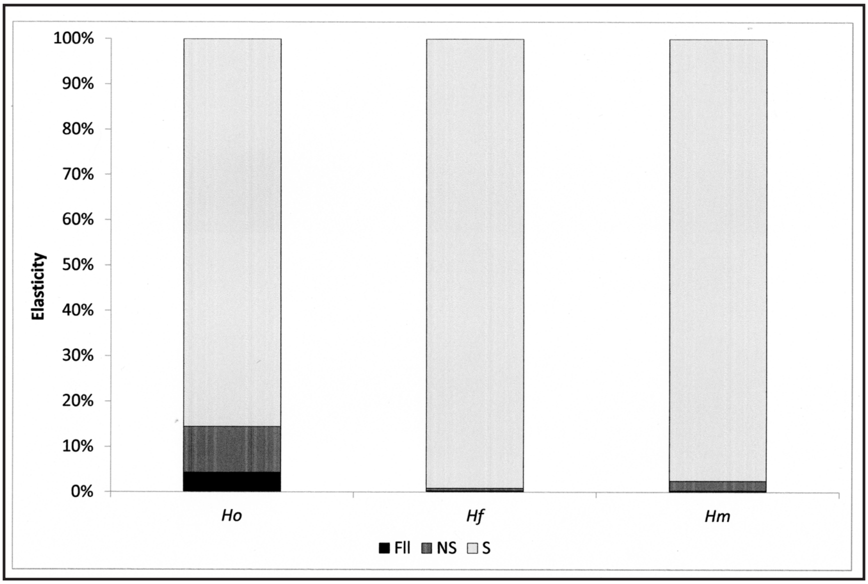
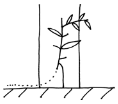
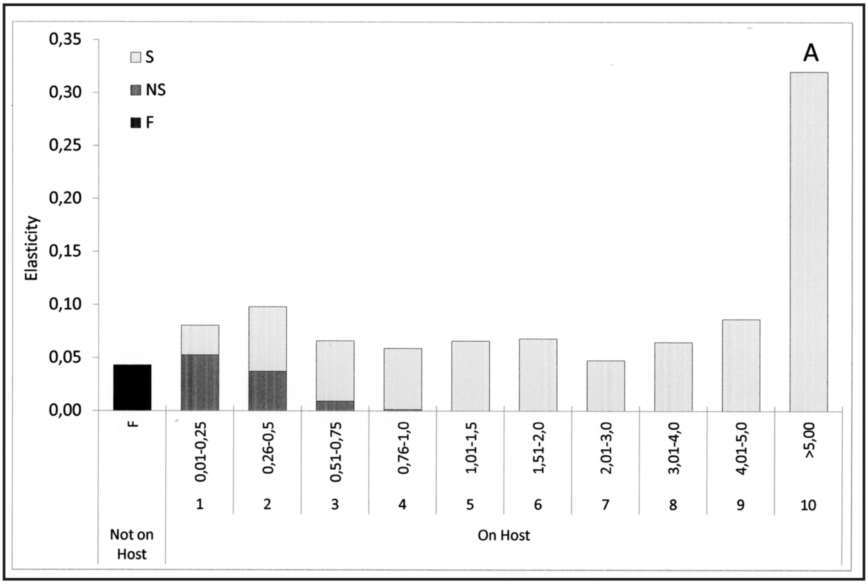


FIGURE 4. Elasticity values of the fallen plants, non-suitable and suitable hosts of the three *Heteropsis* species. *Ho*: *Heteropsis oblongifolia*, *Hf*: *H. flexuosa* and *Hm*: *H. macrophylla*.

According to the matrix elasticity values, population dynamics of the three species depend mainly on the larger stages, the adult plants (Appendix 4A, B & C). However, each species showed its particular differences. For *H. oblongifolia*, the highest elasticity values corresponded to plants on the last stage (> 5 m in upper height). *H. macrophylla* presented the highest values on stages 25 to 30 (> 20 m in upper height) and for *H. flexuosa* the highest values were for the stages 12 to 25 on suitable host (> 7 m in upper height; Fig. 5).

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0,05
0,00
▢ S
▨ NS
■ F
F
0,01-0,25
0,26-0,5
0,51-0,75
0,76-1,0
1,01-1,5
1,51-2,0
2,01-3,0
3,01-4,0
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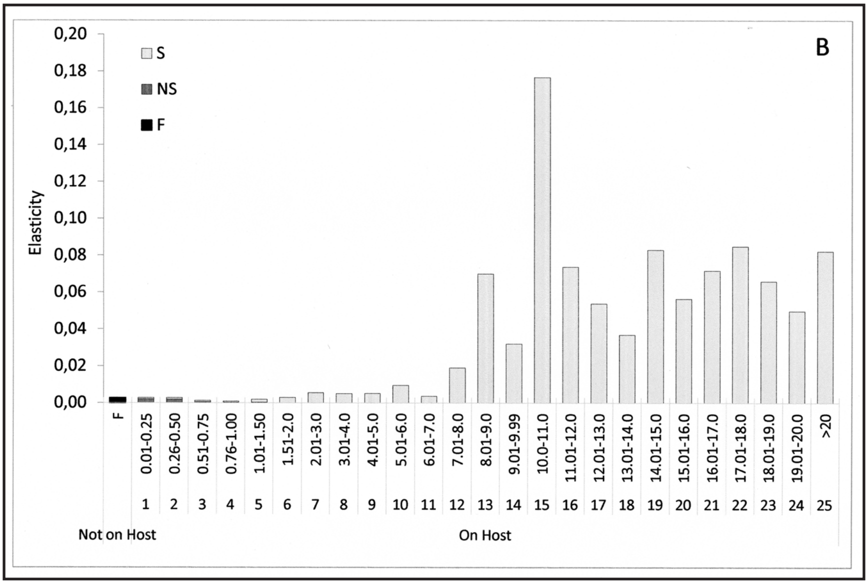
On Host


B
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0,00
▢ S
▨ NS
■ F
F
0.01-0.25
0.26-0.50
0.51-0.75
0.76-1.00
1.01-1.50
1.51-2.0
2.01-3.0
3.01-4.0
4.01-5.0
5.01-6.0
6.01-7.0
7.01-8.0
8.01-9.0
9.01-9.99
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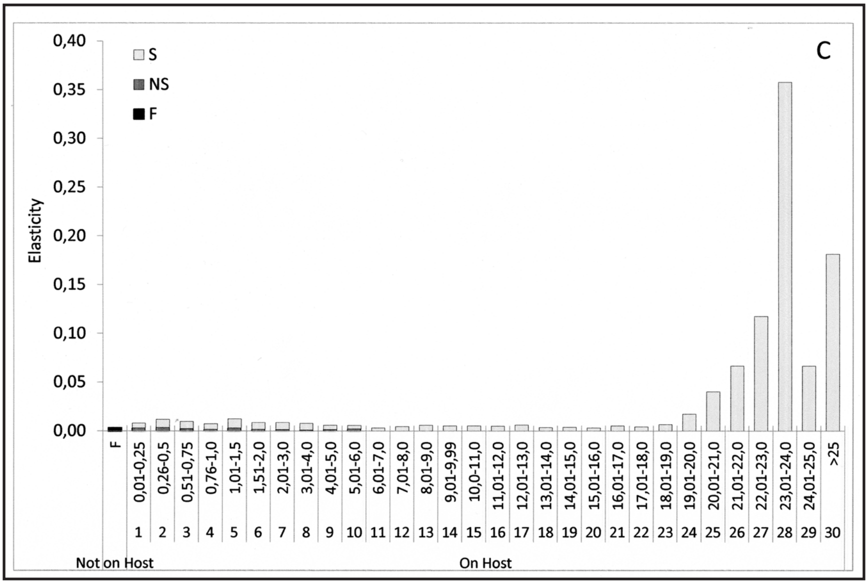
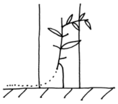


FIGURE 5. Elasticity values of the three *Heteropsis* species. **A)** *H. oblongifolia*, **B)** *H. flexuosa* and **C)** *H. macrophylla*.

LOOP ANALYSIS

A comparison of the loop elasticity values of fallen plants and plants on non-suitable and suitable hosts showed highly similar results for the three species. The life cycle of the three study species (Figure 2) resulted in 97, 228, and 193 loops (the number of loops is equivalent to the nullity, L, for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively. We identified three types of loops: those passing through fallen plant stages, plants on non-suitable hosts and plants on suitable hosts. The percentage of loop elasticity for plants on suitable hosts was by far the highest, with 83.0, 98.7 and 96.8% for *H. oblongifolia*, *H. flexuosa* and *H. macrophylla*, respectively (Figure 6). This finding highlights the relative importance of 'fallen' and plants on non-suitable hosts for *H. oblongifolia*, which had 10 to 13 (fallen) and 7 to 22 (non-suitable) times higher loop elasticity values than *H. flexuosa* and *H. macrophylla*.



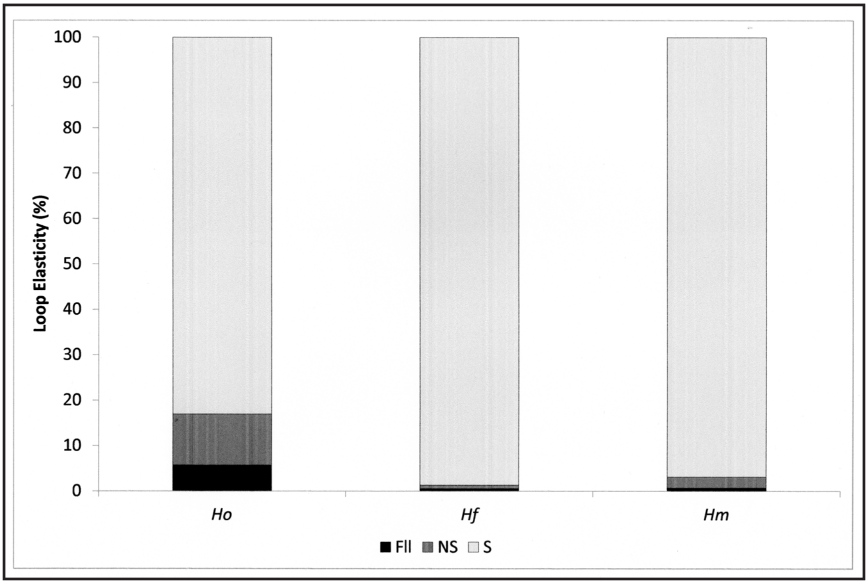
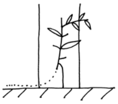
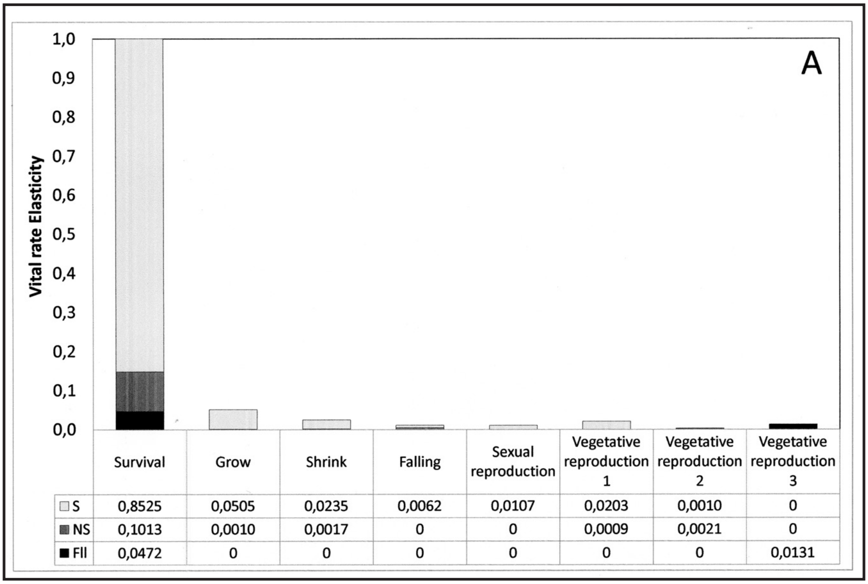


FIGURE 6. Loop elasticity of fallen plants, plants on non-suitable hosts and on suitable hosts. *Ho*: *Heteropsis oblongifolia*, *Hf*: *H. flexuosa* and *Hm*: *H. macrophylla*.

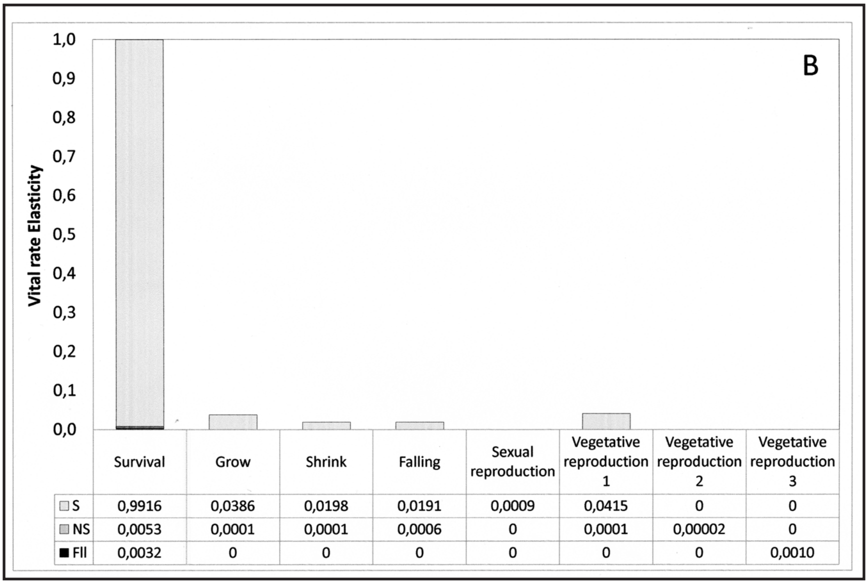
THE RELATIVE IMPORTANCE OF VITAL RATES FOR POPULATION GROWTH

The relative importance of vital rates to **λ** was evaluated by decomposing elasticities at the underlying vital rate level. Vital rate elasticities clearly showed that survival on suitable hosts was more important than other vital rates for the population growth rate (Fig. 7). Growth or progression, shrinkage or retrogression, falling, fecundity and vegetative reproduction of plants on non-suitable and suitable hosts had very low importance to **λ**. Vegetative reproduction was more important to the population growth rate than sexual reproduction. It contributed 0.0374-0.0658, while sexual reproduction just contributed 0.0009-0.0107. Among the three types of vegetative reproduction, segregating in two parts in the same suitable host (*K1*, vegetative reproduction 1) was the most relevant for the three species, contributing 0.0212-0.0650 to the population growth rate; this result was followed by the fallen plants that produced shoots that climbed a non-suitable or suitable hosts and split off (*K3*, vegetative reproduction 3) in *H. oblongifolia* (Fig. 7A).

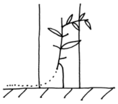


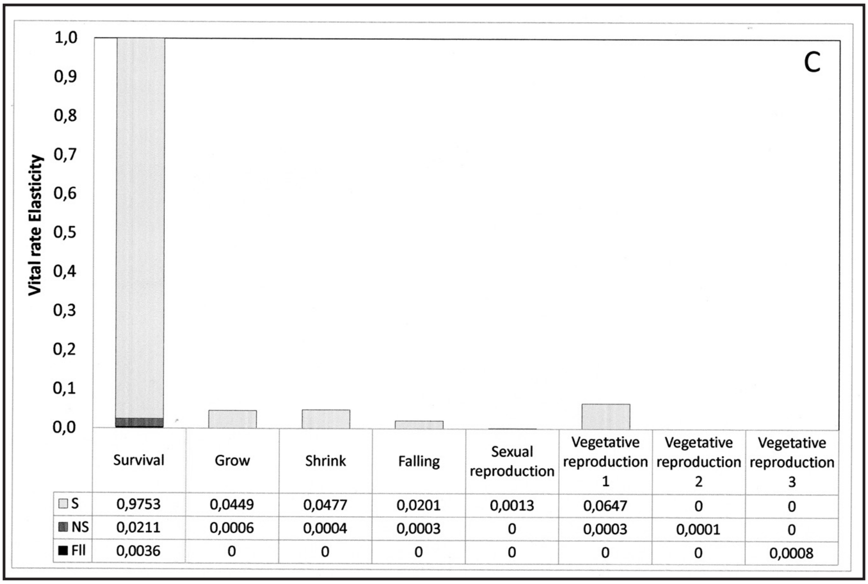


	Survival	Grow	Shrink	Falling	Sexual reproduction	Vegetative reproduction 1	Vegetative reproduction 2	Vegetative reproduction 3
□ S	0,8525	0,0505	0,0235	0,0062	0,0107	0,0203	0,0010	0
▨ NS	0,1013	0,0010	0,0017	0	0	0,0009	0,0021	0
■ FII	0,0472	0	0	0	0	0	0	0,0131



	Survival	Grow	Shrink	Falling	Sexual reproduction	Vegetative reproduction 1	Vegetative reproduction 2	Vegetative reproduction 3
□ S	0,9916	0,0386	0,0198	0,0191	0,0009	0,0415	0	0
▨ NS	0,0053	0,0001	0,0001	0,0006	0	0,0001	0,00002	0
■ FII	0,0032	0	0	0	0	0	0	0,0010





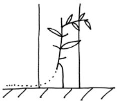
	Survival	Grow	Shrink	Falling	Sexual reproduction	Vegetative reproduction 1	Vegetative reproduction 2	Vegetative reproduction 3
☐ S	0,9753	0,0449	0,0477	0,0201	0,0013	0,0647	0	0
▨ NS	0,0211	0,0006	0,0004	0,0003	0	0,0003	0,0001	0
■ Fll	0,0036	0	0	0	0	0	0	0,0008

Figure 7. Elasticity of vital rates (survival (σ_{ij}), growth (γ_{ij}), shrinkage (ρ_{ij}), falling (π_{ij}) sexual reproduction (f_{ij}) and three different types of vegetative reproduction ($\kappa1_{ij}$, $\kappa2_{ij}$ and $\kappa3_{ij}$)) in Fallen plants, plants on non-suitable and on suitable hosts. **A)** *H. oblongifolia*; **B)** *H. flexuosa* and **C)** *H. macrophylla*.

To determine the importance of the three different types of vegetative reproduction (*K1*, *K2* and *K3*), we set all three vegetative reproduction values to zero in the three matrices. The resulting transition matrices had reduced **λ** values: 1.0034 (95% CI 0.9713 - 1.0319; instead of 1.0446) for *H. oblongifolia*, 0.9853 (95% CI 1.000 – 1.0401; instead of 1.0379) for *H. flexuosa* and 0.9776 (95% CI 1.0000 – 1.0005; instead of 1.0101) for *H. macrophylla*. The differences in **λ** were higher for *H. flexuosa* (5.06%) and lower for *H. macrophylla* (3.21%). Without vegetative reproduction the population growth rates of the three *Heteropsis* species were indeed lower but not different than 1 based on the bootstrap analyses, indicating that the populations would remain stable or increasing. When only *K1* is excluded from the matrices, *H. flexuosa* and *H. macrophylla* showed that **λ** decreased, but they were not significant different than 1 (**λ**Hf =0.9926 (95% CI 1.0000 – 1.0401) and **λ***Hm* =0.9806 (95% CI 1.0000 – 1.0011)). Thus, the population growth rate would not decrease without the three types of vegetative reproduction (*K1*, *K2* and *K3*).

Time To Reach A Reproductive Size And To Be Harvested

H. flexuosa and *H. macrophylla* start to reproduce and be harvested (Chapters 2 and 3) when they reach an upper height of around 10 m, therefore they are confined to suitable hosts. In contrast, *H. oblongifolia* reproduces at 1.5 m height on suitable hosts. Our age-specific calculations showed that reproductive individuals and/or harvestable individuals at



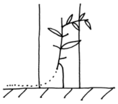
10 m upper height are rather old: the mean age at mean reproduction after finding a suitable host (τ) for *H. flexuosa* and *H. macrophylla* was 58 years, while *H. oblongifolia* was just 28 years.

DISCUSSION

Information on population density, population structure, or other demographic variables is very limited for hemiepiphytes (but see: Williams-Linera & Lawton 1995, Chapter 2), even for rather well studied woody taxa such as primary hemiepiphytes (Todzia 1986, Michaloud & Michaloud-Pelletier 1987, Putz & Holbrook 1989, Daniels & Lawton 1991). In spite of the ecological role and economical importance (Balcázar-Vargas & van Andel 2005, Wallace, Pereira & Plowden, 2011), very little is known about the ecology and demography of secondary hemiepiphytes (Williams-Linera & Lawton 1995, Hoffman 1997, Plowden 2001, Knab-Vispo 2003, Chapter 2). As far as we know, this is the first demographic study on this group of plants.

The vital rates of the different life history stages (used to calculate the entries of the population projection matrix) determined the patterns of the stable-stage distribution (SSD) and reproductive values (**v**). OSDs were reasonably close to the SSDs in the three studied species, indicating that the analysis of the asymptotic dynamics was relevant to the characterization of the demographic environment at a given point and time (Caswell 2001, Williams et al. 2011). The SSD were dominated by individuals in the first two categories on non-suitable and suitable hosts. *H. flexuosa* and *H. macrophylla* presented a higher number of individuals per ha on non-suitable than on suitable hosts. In contrast, *H. oblongifolia* presented an inverse behavior, where there were more individuals on suitable than on non-suitable hosts. We offer two non-exclusive explanations for such a pattern: first, there is a larger proportion of suitable hosts in the forest for *H. oblongifolia*, as small trees are more abundant (e.g., Duivenvoorden 1994, Phillips & Miller 2002) and second, *H. oblongifolia* produces ramets at a higher rate and the more vigorous clonal propagation of this species may increase the chance that established seedlings and juveniles are present on suitable hosts. As a result, the proportion of established seedlings and juveniles of *H. oblongifolia* on suitable hosts was higher than that of the other two species (Chapter 2). *H. flexuosa* and *H. macrophylla* have 23 and 2 individuals per hectare, respectively. Hoffman (1997) and Plowden (2001) reported the density of trees with *H. flexuosa* adult plants in Guyana and Brazil, which varied from 61 to 232 to 143 to 453 host trees/ha respectively. Our results are more similar to those found by Durigan (1998) in Brazil, which reported 1.4–5.3 *H. flexuosa* host tree/ha. The results are difficult to compare due to these authors did not attempt to count the number of individual plants established per host tree.

Our results, as indicated by the calculation of population growth rates (**λ**), suggest that the populations of the three study species would grow slowly if the vital rates remained unchanged under the studied environmental conditions. In general, long-lived species have **λ** values close to unity, including cacti (Esparza-Olguín et al. 2002, 2005), lianas (Nabe-Nielsen



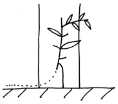
2004), rattans (Bøgh 1996, Binh 2009), epiphytes (Zotz 2005, Zotz, Laube & Schmidt 2005, Pfeifer et al. 2006, Mondragon 2009), palms (Bernal 1998, Olmsted & Alvarez-Buylla 1995) and trees (Zuidema & Boot 2002, Guedjea 2003, Alvarez-Buylla et al. 1996). The dynamics of the three *Heteropsis* species were most strongly determined by large plants. In general, many long-lived species with $\boldsymbol{\lambda}$ values close to unity have this type of elasticity pattern (Silvertown et al. 1993, Alvarez-Buylla et al. 1996, Esparza-Olguín et al. 2002, Mendez et al. 2004, Nabe-Nielsen 2004, Zotz 2005).

The Role Of Host Suitability

According to the elasticity and loop analyses plants on suitable hosts have the highest importance for population growth rates, even though the largest percentage of recruits (70-85%) initially climbs non-suitable hosts. It is remarkable that the populations of the three *Heteropsis* species still grow, despite their low levels of recruitment due to high seedling mortality on the ground, their random strategy to find a host, and the very low density of suitable hosts (Chapter 2). Therefore, low reproductive success, seen here as the probability of a seedling to climb a suitable hosts (or to find a suitable habitat), apparently does not hamper population maintenance and growth for these species, as has been reported for other species (García 2003). The key to the maintenance of these populations is probably the long reproductive lifespan of these species (age at reaching the last category: *H. oblongifolia*= 71, ±SD 86 *H. flexuosa*= 52, ±SD 91 and *H. macrophylla*= 16, ±SD 24 years).

Source And Sink Dynamics

We found evidence for strong source-sink dynamics for the three *Heteropsis* species. The ramets and recruits climbed preferably on non-suitable hosts and as the non-suitable sub-populations (sinks) with $\boldsymbol{\lambda}<1$ when recruitment into these sub-populations was blocked. About 64-74% of the ramets and 72-81% of recruited seedlings were climbing non-suitable hosts (Chapter 2). These high percentages are most likely due to the random searching strategy of seedlings and to the very low density of suitable host (Chapter 2). Our results are comparable to those of studies on recruitment of tree species which showed strong recruitment subsidies to unfavorable habitats (Kaneko, Takada & Kawano 1999, Kaneko & Kawano 2002, Zuidema et al. 2010). Also for these tree species, blocking recruitment subsidies to non-preferred habitats led to population decline. In conclusion, the growth of the *Heteropsis* populations depends much on the restricted recruitment of individuals on suitable hosts. This is confirmed by the elasticity and loop analyses, which showed that the contribution of the sub-populations on suitable hosts were by far the largest for the three species.



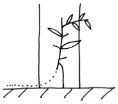
VITAL RATES IMPORTANCE TO POPULATION GROWTH RATES

The most important vital rate for the population growth of the three *Heteropsis* species was survival on suitable hosts while values for sexual reproduction and growth were low. Similar results are mostly found for woody plants of forest habitats (Caswell 2001, Silvertown et al. 1993, Silvertown & Franco 1993, Pino, Picó & Roa 2007).

Our study species reproduced both sexually and vegetatively during the study period. The three modes of vegetative reproduction were far more important: they contributed 3 to 50 times more to population growth than sexual reproduction. Population dynamics of many species may depend heavily on vegetative reproduction (Eriksson 1992, Silvertown et al. 1993, Mandujano et al. 2007, Clark-Tapia et al. 2005) whilst others found evidence of high sexual reproduction and repeated recruitment from seeds (Guàrdia et al. 2000, Berg 2002). Nevertheless, these reproductive modes are relatively unimportant compared to survival. A perturbation analyses that involved complete cessation of clonal reproduction (*K1*, *K2* and *K3*) confirmed the low importance of vegetative reproduction to $\boldsymbol{\lambda}$. The population growth of these species does not depend on *K2* (probability that an individual produced a ramet that descended to the ground and then climbed a host and split off) and *K3* (probability of a fallen plant producing shoots that eventually climbed a non-suitable or suitable host and split off). This means that the strategy of ramet production to search for a new host is in fact of very little importance to population growth, suggesting that most of the individuals on the non-suitable hosts are 'lost cases' because they do not contribute much to population growth rate.

HOW LONG DOES IT TAKE TO BECOME AN ADULT (AND HARVESTABLE)?

The epiphytes' habitat is very dynamic. Therefore, it was expected that these plants respond to this selective pressure, showing an early reproductive maturity (Benzing 1978). However, a *H. oblongifolia* seedling (after finding a suitable host) would require about 28 years to reach its reproductive size (1.5 m height). The canopy species *H. flexuosa* and *H. macrophylla* would need around 58 years to reach its reproductive size (10 m height). All three study species continued to grow after reaching their reproductive size. Hoffman (1997) reported very similar results for *Heteropsis flexuosa* in Guyana. Comparisons between secondary hemiepiphytes and other plants are difficult due to differences in architecture and life form. Benzing (1981) estimated that the bromeliad *Tillandsia circinnata* required 8 to 10 yr to reach its reproductive size. Zotz (1995) calculated that the epiphytic orchid *Dimerandra emarginata* needed 10 yr to be potentially reproductive and about 25 yr to reach maximum size. Gerwing (2004) calculated for two late successional lianas species that the estimated time taken to attain 5 cm diameter ranged from 13 to 50 years for *Bauhinia guianensis* to 30 to 169 years for *Memora schomburgkii.*



H. flexuosa and *H. macrophylla* are two useful species employed in the cultural artifacts and craft market around the Amazon (Balcázar-Vargas & van Andel 2005, Plowden et al. 2003). They can be harvested when they reach an upper height of around 10 m on a suitable host (the roots are enough thick and long; Balcázar-Vargas & van Andel 2005, Chapter 3), when they are around 58 years. *H. flexuosa* and *H. macrophylla* showed very slow growth (ca. 8 cm / year) with large variation, and a substantial percentage (*H. flexuosa* = 44; *H. macrophylla*= 31%) did not grow or shrink (Chapter 3). This variation may strongly affect population dynamics (Zuidema & Franco 2001, Zuidema et al. 2009). If it is maintained over time, persistently fast growers will have a greater chance to reach this size (assuming equal annual mortality risks) and will do so at a younger age than slower growers (Zuidema et al. 2009). At present, we do not know whether growth differences persist over time. To conclude, *Heteropsis* is characterized by a long lifespan (mean lifespan: *H. oblongifolia*=121, *H. flexuosa*= 37 and *H. macrophylla*=71 years). Given these very slow growth rates and the high age at harvestable size, there is little scope for cultivation as an alternative to harvesting roots (for craft industry) from natural populations in *H. flexuosa* and *H. macrophylla*. Based on these results, we strongly advise that harvesters prevent killing plants (e.g. by cutting all the adventitious roots) or pull down the entire plants during root harvesting.

ACKNOWLEDGMENTS

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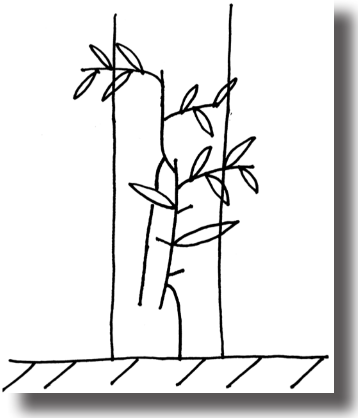
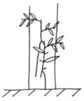
Drawings by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Cauqetá, 1998. In the center Bartolome Castro weaving a creel (to'naaru) (Huitoto)

Chapter 5

General summary and discussion





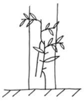
General summary and discussion

The ecology of hemiepiphytes is very poorly understood. The general life history of primary hemiepiphytes is quite well described, but ecological studies have mostly ignored secondary hemiepiphytes so far (Williams-Linera & Lawton 1995). More appalling is the lack of information on hemiepiphyte vital rates and demography. Such information is essential to truly understand the ecology, management and conservation of this group that is an important component of tropical forest canopies. In this thesis, I aimed to fill some of these gaps in knowledge on hemiepiphyte ecology. I studied three sympatric secondary hemiepiphyte species in the Colombian Amazon: *Heteropsis flexuosa* (Kunth) G.S. Bunting, *H. macrophylla* A.C. Sm and *H. oblongifolia* Kunth. I first evaluated how seedlings of these species find a host (chapter 2) and whether these hosts are suitable (i.e. sufficiently tall) or not. Then, I described and explained patterns of survival, growth, retrogression, vegetative and sexual reproduction for these species, and the effect of host suitability on these vital rates (chapter 3). Next, I analyzed the relative importance of suitable hosts (those that are sufficiently tall to allow *Heteropsis* reproduction) and non-suitable hosts (those that are too low) on the demography of my study species. Finally, I estimated the age at which *Heteropsis* species become reproductive and at which their roots can be harvested to be used for craft production (chapter 4).

THE LIFE CYCLE OF A SECONDARY HEMIEPIPHYTE (*HETEROPSIS*)

The Quest for a Host - The life cycle of secondary hemiepiphytes has two contrasting phases. The first occurs after germination and ends when the seedling climbs a host. Secondary hemiepiphytes lack the capacity to hold themselves upright, and therefore they need to encounter suitable structures on which to climb (Putz & Holbrook 1991). This requires an effective searching strategy, and ideally one that directly results in a host tree that can sustain the climber throughout its life (Putz 1984).

Searching strategy - One of the most intriguing questions in climbing plant ecology is how vines, lianas and secondary hemiepiphytes find a suitable host (Strong & Ray 1975). Over the last 130 years, various hypotheses have been put forward. The first was Charles Darwin (1875), who presented the results of his experiments on the vine *Bignonia capreolata* L., and stated that hosts were found by “apheliotropism” (growth away from light). Since then, several other mechanisms have been suggested for lianas and vines, including negative geotropism (growth away from gravity) by Menninger (1970), random searching (Hottes 1933), thigmotropism (growth in response to mechanical contact) by Darwin (1875) and Jaffe & Galston (1968) and positive phototropism (growth to a light stimulus) by Janzen (1969). Strong and Ray (1975) showed in an experimental study that seedlings of the secondary hemiepiphyte, *Monstera gigantea* (Roxb.) Schott, found hosts by



growing towards the darkness of a tree silhouette, a mechanism that they termed skototropism (Strong & Ray 1975) and Kaufman et al. (1989) called negative phototropism. Since then, this topic has not been studied. I studied the host-searching behavior in *Heteropsis* and found that the searching of stems or shoots was often erratic: they were growing in random directions and could also change course without noticeable cue (e.g., changing light conditions, physical obstruction). Virtually no seedling was growing in a straight line and I sometimes found clumps of seedlings together, coming from seeds of the same infrutescence, growing in very different directions (Fig. 1). Although these are merely field observations that lack measurements and statistical tests to determine whether the growing direction of seedlings was in fact random, these preliminary observations suggest that host searching is a random process. My field observations on *Heteropsis* seedling growth contrast those of Strong and Ray (1975) on *Monstera gigantea*. If growth of the three *Heteropsis* seedlings species would be governed by skototropism, I would have found most of the recruited seedlings from the same infructescence growing in the same direction, instead of radiating in different directions. Furthermore, I would have expected to find *Heteropsis* seedlings to climb the parent tree or large trees and not the smallest hosts in the forest, as in fact it was found, the majority of *Heteropsis* seedlings climbed up on very small and non-suitable hosts (Chapter 2). Even when *Heteropsis* seedlings germinate close to the supposed host tree of their mother plant, most of them will climb up on a non-suitable host. In contrast, seedlings of *Monstera* grew back to the host tree of their mother plant (Ray 1976).

I found a stronger and formal confirmation of this random search behavior by comparing the diameter distribution of hosts of *Heteropsis* seedlings that had just climbed a host, to that of all trees, palms, and lianas of ≥10 cm dbh in the plots. These diameter distributions were very similar, suggesting that search behavior is random. In contrast, when considering the diameter distributions of host for *Heteropsis* juveniles and adults, these distributions differed significantly from that of all trees, palms, and lianas ≥ 10 cm dbh in the plots. *Heteropsis* juveniles and adults occurred mainly on trees, palms, and lianas with dbh ≥ 20 cm. Furthermore, the percentage of seedlings present on host of 10–19 cm dbh was greater than the percentage of juveniles and adults in that category. These results were consistent for the three species and seem to suggest that *Heteropsis* seedlings climb up a randomly encountered, nearby host, and that they adopt a random searching strategy instead of one directed by skototropism (Chapter 2). Once *Heteropsis* seedlings climb on non-suitable hosts, they change hosts via vegetative reproduction.

Mortality risk on the forest floor - The leafless, non-climbing seedlings experience a high mortality risk (72% per year; Chapter 2 and 3, Fig. 1A y B) caused by falling debris and the depletion of seed resources before finding a host (Ray 1976). Non-climbing *Heteropsis* seedlings are still attached to their seeds and lack leaves to photosynthesize. This makes them vulnerable to exhaustion of reserves and limits their ability to recover from damage, so they cannot survive for long periods. However, a non-climbing seedling generally survives sufficiently long to reach spots within 1 m of their place of germination.

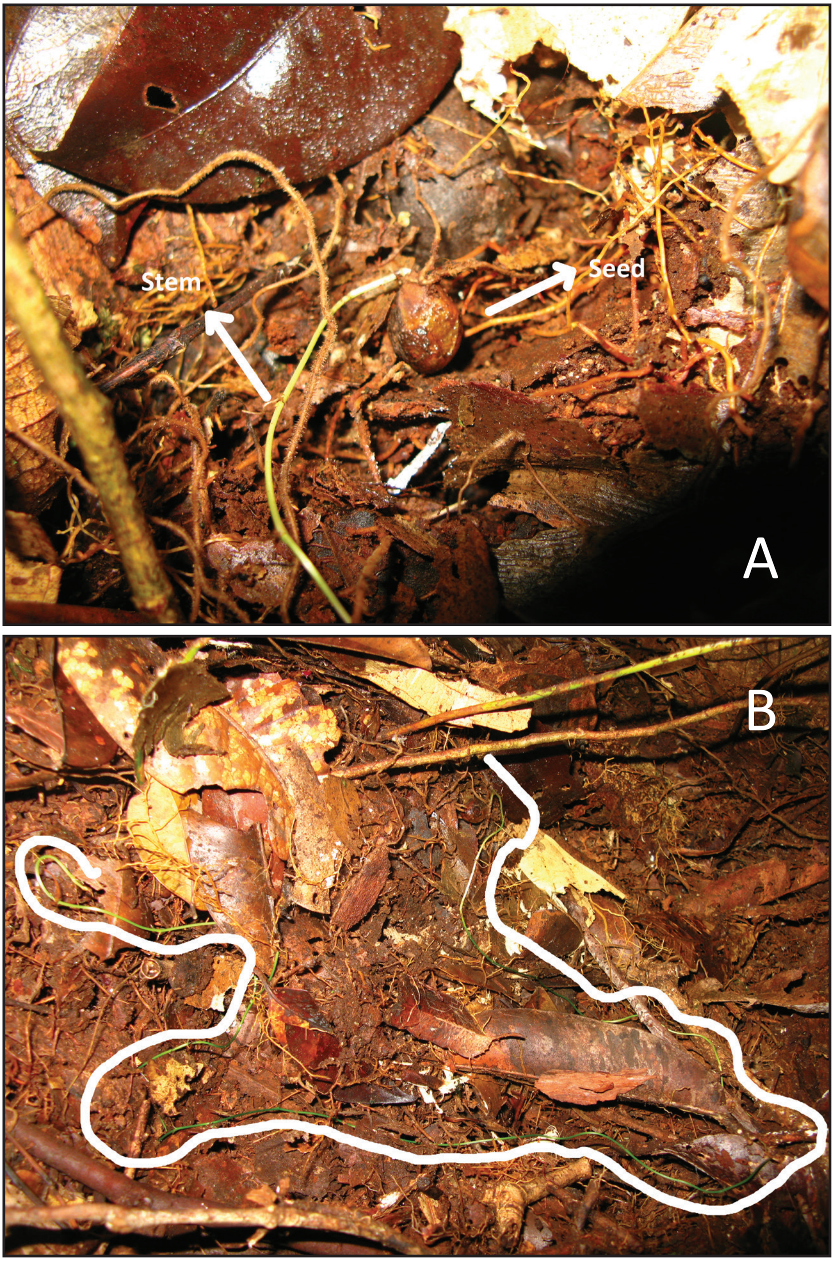
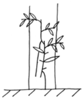


FIGURE 1. A) Detail of a germinated seed. Seed size: length= 1.7 cm * width= 1.2 cm. **B)** Seedling of *Heteropsis flexuosa* after germination. The leafless stem moves away from the germination spot. The white line shows the direction taken by the *Heteropsis* stem on the forest floor (photos: M.P. Balcázar-Vargas).

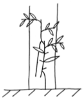


THE ROAD TO THE CANOPY

The second phase of the *Heteropsis* life cycle starts when a host has been found and the plant ascends, attaching itself with adventitious anchoring roots (Wilder 1992, Romero 1994; Fig 2A). Once attached, the plant produces a second type of roots: absorbing roots that take up water and nutrients from the soil (Fig 2A). Once these absorbing roots are functional, the lower part of the stem dies and the plant loses the initial connection with the forest floor and what is left of the seed (Fig. 2). Next, the plant produces plagiotropic branches (horizontal branches bearing leaves in planes along each axis, Fig. 3) and more absorbing roots. In this process, the lower parts of the stem senesce together with the lowest roots (Putz & Holbrook 1986, Plowden et al. 2003), until the plant reaches the understory (*H. oblongifolia*), the sub-canopy (*H. flexuosa*) or the canopy (*H. macrophylla*).

Troubles to reach the canopy: The wrong host! - Probably due to the random searching strategy and the low density of suitable hosts, the vast majority of *Heteropsis* seedlings climb up very small and non-suitable hosts (81%). As a consequence, those individuals cannot complete their life cycle; the reproduction of *Heteropsis* species is height dependent (Fig 4 Chapter 2 and 3). Many ‘hosts’ of the study species were dead plants, herbs, or tree seedlings. In fact, the *Heteropsis* seedlings climb everything that they find in their path, even fallen leaves. This finding is consistent with the results of various studies on host tree characteristics of tendrillate lianas (Putz 1984, Putz & Holbrook 1991, Nabe-Nielsen 2001, Sakai et al. 2002). As for most lianas (Putz 1984, 2012) and a climbing fern, *Polybotrya pubens* Mart. (Young and León 1991), suitable hosts are a limited resource for the three *Heteropsis* species; therefore, the chances to find a suitable host are slim (Chapter 2).

Once on the wrong host, what does the plant do? Since the vast majority of the *Heteropsis* seedlings climbs non-suitable hosts, they need to search for a new host. Clonal propagation via shoot production allows *Heteropsis* to move from a non-suitable host to a suitable one (Figure 5 B; Chapter 2). Flagelliform shoots have been interpreted as a mechanism for overcoming limiting conditions in the plant’s exploitation of its habitat (Andrade and Mayo 2000). Every year, between 0.6 and 2.4 percent of the *Heteropsis* individuals produce shoots (ramets) that search for new hosts; most of them climbed (again) on a non- suitable host (Chapter 2). However, the proportion of ortets (genets) on suitable hosts did increase after ramet production, because in 35 to 46 percent of the cases, at least one of the ramets climbed a suitable host. This means that these long-lived plants probably need to produce a large number of ramets to guarantee that one of them finds a suitable host that allows the genetic individual as a whole to reproduce. This phenomenon shows that the host tree searching does not stop at the seedling category. It is a repetitive trial and error searching method through clonal propagation, until the plant climbs up a suitable host and reaches its desired height in the (sub-)canopy (*H. flexuosa* and *H. macrophylla*) or the understory (*H. oblongifolia*).



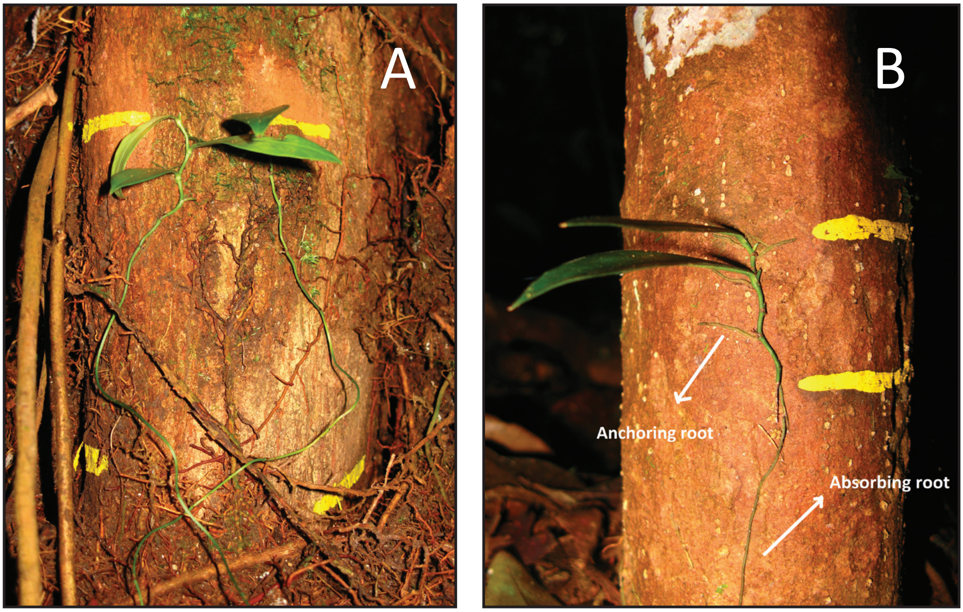


Figure 2. **A)** *Heteropsis flexuosa* climbing seedling no yet possessing absorbing roots. **B)** *H. flexuosa* climbing seedling with absorbing and anchoring roots (photos: M.P. Balcázar-Vargas).

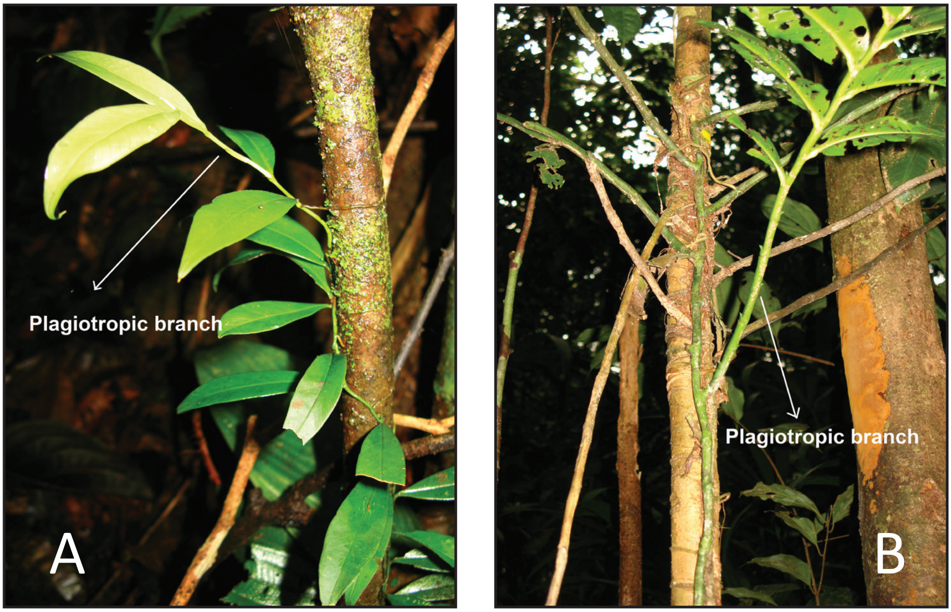
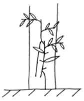


Figure 3. A) *H. flexuosa* climbing seedling showing the first plagiotropic branch. **B)** H. tenuispadix climbing plant (species not included in this study) showing several plagiotropic branches (photos: M.P. Balcázar-Vargas).



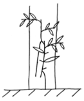
REACHING THE CANOPY

The vital rates of Heteropsis species - While there have been recent advances in quantifying vital rates of lianas, vines, rattans and epiphytes (e.g. Nabe-Nielsen 2004, Zotz 2005, Gilbert et al. 2006, Kouassi et al. 2008, Binh 2009), such knowledge is lacking for hemiepiphytes (Williams-Linera & Lawton 1995). I provide basic insights into the vital rates (survival, growth, vegetative propagation and sexual reproduction) of three *Heteropsis* species and explore what factors govern their performance. To my knowledge, this is the first study providing such insights into hemiepiphyte ecology. Characteristics of the study species are given in Table 1.

FIGURE 4. A non-suitable host denoted by an arrow in its apical stem.

Survival - Once the three *Heteropsis* species ascended a host their survival probability increased enormously (94-85%, Table 1), a phenomenon also observed among lianas (Nabe-Nielsen 2004, Gerwing 2004). *Heteropsis* (like other secondary hemiepiphytes) are appressed to the trunk (Fig 2) which may reduce damage and mortality from falling debris (Ray 1976).

Growth - I had two hypotheses about the height growth rate; the first was related to how fast *Heteropsis* plants can grow and the second was related to how this rate changes with size. My first hypothesis suggested that these plants should be able to attain high rates of extension growth as lianas and rattans, because 1) their stems have only a limited support function and biomass allocated to them can be invested in stem extension rather than in rigidity and stoutness (Bell et al. 1988; Darwin, 1867; Putz 1984, den Dubbelden & Verburg 1996). 2) The epiphytes' habitat is very dynamic, therefore, it might be expected that these plants respond to this selective pressure, showing high growth rates, an early reproductive maturity and abundant seed production (Benzing 1978). 3) Secondary hemiepiphytes have absorbing roots that allow them to connect to the soil and uptake water and nutrients continuously (Croat, 1981). My second hypothesis expected that as these plants ascend to the canopy, growth rates increase. As they will have more and thicker absorbing roots, more plagiotropic branches and greater access to light, they can obtain more water and nutrients and photosynthesize more. However, my results did not lead to adopting these hypotheses: all three *Heteropsis* species grew very slowly in height (ca. 2 - 8 cm/year) with a substantial



number of individuals (up to 62 %) not growing at all or shrinking over a two-year period (Chapter 3, Table 1) and the increase in the growth rate occurred, but it was not as strong as I expected. These findings also contrast strongly with growth rates of rattans and lianas (Bøgh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, 1990b, Schnitzer 2005). The slow growth of secondary hemiepiphytes is possibly explained by the limited amount of nutrients and water that can be taken up by the absorbing roots, but this remains speculative.

I found that the amount of light and the number of roots positively affects growth rates to some extent in one of my study species, *Heteropsis macrophylla*. Similar relations for growth and light have been found for the shade-tolerant lianas Machaerium cuspidatum Kuhlm. & Hoehne and Connarus turczaninowii Triana (Nabe-Nielsen 2002, Aide and Zimmerman 1990), and for six rattan species (Binh 2009, Bøng 1996). Although height growth in *Heteropsis* is certainly light-limited, water and nutrients shortage may play an additional role, suggested by the effect of the number of absorbing roots on height growth rate. New studies showed that as adult *Heteropsis* plants ascend in height on a host, both the number as the thickness of the absorbing roots increases. As a result the hydraulic efficiency improves, i.e. the amount of water that can pass through a certain structure (root, stem, petiole) per unit of time and pressure gradient (Martínez-Vilalta and Piñol 2003, Gil-Pelegrín et al., 2005, Burgess et al., 2006). In other words, as the roots increase their diameter, they are able to transport more water and therefore to sustain a bigger amount of biomass (Turriago *pers. comm.*).

A large proportion of seedlings belonging to the genus *Heteropsis* and tendrillate lianas climb up on non-suitable hosts where they cannot complete their life cycle (Putz 1984, Putz & Holbrook 1991, Nabe-Nielsen 2001, Sakai et al. 2002, Balcázar-Vargas et al. 2012). Because individuals on non-suitable hosts lack sufficient vertical support, they will tend to invest more resources in producing shoots that move downwards searching for new hosts. Therefore, I expected that plants on suitable hosts would grow faster in height than those on non-suitable ones. However, no significant differences in the upper height growth rates between plants on these two types of hosts were found in any of the species. In contrast, lianas were found to grow two to seven times faster when suitable supports were experimentally provided (Putz 1984). To sum up, the suitability of the host did not affect survival and growth of the three *Heteropsis* species in the short term.

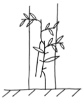
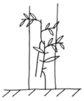


Table 1. Comparisons of the three studied *Heteropsis* species. **Seedlings**: *H. oblongifolia*: individuals with an upper height from 0.01 to 0.50 and for *H. flexuosa* and *macrophylla* from 0.01 to 1.00 m on non-suitable and suitable host. **Juveniles**: *H. oblongifolia*: individuals with an upper height from 0.51 to 1.49 and for *H. flexuosa* and *macrophylla* from 1.01 to 9.99 m on non-suitable and suitable host. **Adults** *H. oblongifolia*: individuals with an upper height ≥1.5 and for *H. flexuosa* and *macrophylla* ≥10 m on suitable host. Mean values of abundance are given. Mean height growth rate includes individuals with negative, no and positive height growth. Mean positive height growth rate include only individuals with positive height growth. The importance of life stages and vital rates is based on elasticity analysis of matrix population models (chapter 4).

Species	***H. oblongifolia***	***H. flexuosa***	***H. macrophylla***
General characteristics			
Maximum Adult height [m]	14	25	35
Reproductive size [m]	≥ 1.5	≥ 10	≥ 10
Reproduction	Seed & vegetative	Seed & vegetative	Seed & vegetative
Total abundance [ha-1]	125	569	102
Mean growth rate in upper height [m per yr-1]	0.0208	0.0768	0.0797
Maximum growth rate in upper height [m per yr-1]	0.8051	2.7830	2.9308
Mean positive height growth rate [m per yr-1]	0.1333	0.1953	0.2032
Seedlings mean positive height growth rate [m per yr-1]	0.0444	0.0424	0.0468
Juveniles mean positive height growth rate [m per yr-1]	0.1963	0.2626	0.2478
Adults mean positive height growth rate [m per yr-1]	0.2938	0.5720	0.7141
Abundance of fallen individuals [ha-1]	9	9	4
Abundance of individuals on non-suitable host [ha-1]	36	360	63
Abundance of individuals on suitable host [ha-1]	80	201	36
Abundance of seedlings [ha-1]	65	455	63
Abundance of adults or harvestable individuals [ha-1]*	17	23	2



Species	*H. oblongifolia*	*H. flexuosa*	*H. macrophylla*
Percentage of recruitment of individuals on non-suitable host [% y-1]	85	70	73
Percentage of recruitment of individuals on suitable host [% y-1]	15	30	27
Regeneration strategy	Shade-tolerant	Shade-tolerant	Shade-tolerant
Population dynamics			
Population growth rate (λ)	1.0446	1.0379	1.0101
95% bootstrap confidence interval	1.0025 - 1.1230	1.0000 - 1.2069	1.0000 - 1.1002
Non-climbing seedlings survival [% y-1]	-	28	28
Climbing seedling survival [% y-1]	90.9	83.7	95.1
Adult survival [% y-1]	99.5	99.9	95.6
Fallen individuals survival [% y-1]	72.4	67.9	78.6
Plants did not change in size at all or shrunk during two years [%]	62	44	31
Proportion of reproductive adults [%]	10.7	35.4	49.1
Most important state	Plants on suitable host	Plants on suitable host	Plants on suitable host
Most important life stage [upper height in m]	≥ 5	> 7	> 20
Most important vital rate	Survival on suitable host	Survival on suitable host	Survival on suitable host
Mean life span [yr]	121	37	71
Age to reach adult state [yr]	28	58	58

*: *Heteropsis flexuosa* and *macrophylla* are harvestable species from ≥ 10 m upper height. *H. oblongifolia* is not a harvestable species and becomes reproductive above 1.5 m.

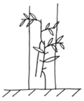
Fecundity - Like many other species, *Heteropsis* species must reach a threshold size before beginning to reproduce (Gross 1981, Klinkhamer et al., 1987, Ohlson 1988, Primack & Hall 1990, Méndez & Obeso 1993). The (sub-) canopy species: *H. flexuosa* and *H. macrophylla* become reproductive or produce inflorescences at ≥ 10 m while *H. oblongifolia* at ≥ 1.5 m (Chapter 2, Table 1). For the canopy species, the probability of inflorescence production increased with the number of plagiotropic branches and the upper height. Thus, plants with the same upper height but with more branches might produce more inflorescences, because they are only produced on those branches. On the other hand, the number of the inflorescences produced per plant was not significantly related to upper height in two of the three species.

Once in the canopy, problems are not over

Epiphytes and hemiepiphytes occupy a highly dynamic substrate. The substrate may slowly increase in height as the host grows or be suddenly destroyed when the host falls (Zotz 1998). Once the host has fallen, survival on the forest floor is frequently brief for epiphytes (Matelson et al. 1993). By contrast, *Heteropsis* individuals can survive after falling down from or with a host: up to 78 % of such fallen individuals survive, I do not know specifically how many years a *Heteropsis* plant can live on the ground, but few individuals were some cm below the litter continuously producing ramets, meaning that some of them are able to live for years on the ground. As such fallen *Heteropsis* individuals behaved comparable to rattans (Putz 1990a) and lianas (90% survival; Putz 1984). After falling, the three *Heteropsis* species showed a high incidence of sprouting, especially in *H. oblongifolia* (46%). Although fallen epiphytes may not die immediately, their chance of ever producing successful progeny is virtually zero (Hietz et al. 2002). Lianas, however, vigorously sprout after falling in natural and selectively logged forests (Putz 1984, Appanah and Putz 1984). In this respect, the *Heteropsis* species studied behave more like lianas. This has consequences for their lifespan, as this is not limited by that of host. Hemiepiphytes individuals (genets) that have the capability to survive after falling and to produce new ramets (branches) that climb up new hosts, will be able to survive the death of a host. As a conclusion, *Heteropsis* species appear to have a high resilience to host falling. Together with high annual survival rates (Table 1) and high incidence of sprouting after falling, this suggests that genets of these species may reach high ages. Indeed, age estimates based on matrix models show that *Heteropsis* ramets are characterized by life spans of 37-121 years (Table 1), suggesting that this will be considerably higher for genets.

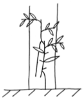
Demography of three *Heteropsis* species

In the previous section, I showed that most of the vital rates did not differ across my study species or host types. However, as very many recruited seedling climb onto non-suitable host and as these plants may be able to reach suitable hosts through clonal reproduction, it is still possible that this lifecycle pathway through non-suitable hosts contributes substantially to the population growth rate (**λ**). Consequently, in this section, I evaluate the demographic consequences of host suitability based on three different analyses: elasticity (de Kroon et al. 1986; 2000; Caswell 2001), loop analyses (Güneralp 2007) and source and sink dynamics (Pulliam 1988; Hanski 1999). This is a topic that has not been studied so far in any climbing plant.



The significance of host suitability - To evaluate the role of host types (non-suitable and suitable) on **λ**, I carried out elasticity and loop analyses. According to these analyses, plants on suitable hosts have the highest relevance for **λ**. Thus, the small proportion of seedling that climb up on suitable host (19- 28%) and survive until they reach a reproduction state contribute more to **λ** than the large share of the seedlings that climb onto non-suitable hosts. The three *Heteropsis* species populations still grow, despite the random strategy to find a host, the high seedling mortality on the ground and the very low density of suitable hosts that finally results on very low levels of recruitment on this kind of host (Chapter 2 and 3). The key to the maintenance of these populations is probably the long reproductive lifespan of these species.

Source and Sink dynamics - A common feature of all source-sink models is that differences between habitats are extreme. In the high quality habitat (the source), individuals have an average fitness greater than one and this population, on average, has a $\lambda \geq 1$. The poorer quality habitat (the sink) is so poor that individuals have an average fitness less than one and in the absence of immigration, the population declines towards extinction (Diffendorfe 1998, Pulliam 1988; Hanski 1999). At demographic equilibrium (or over long time periods), source-sink models predict that the source habitat is a net exporter of individuals, whereas the sink habitat is a net importer of individuals. Adapting the theory of source-sink dynamics to secondary hemiepiphytes, individuals on suitable and non-suitable hosts can be seen as separate sub-populations. For practical purposes, I use the term sub-populations here, to define the set of plants that climb either on non-suitable or suitable hosts. Individuals on suitable hosts act as a source sub-population since they are able to reproduce and produce offspring, while those on non- suitable hosts act as sink sub-populations because they would go “extinct” in the absence of reproduction coming from the source sub-population on suitable hosts. Consequently, when individuals move from non- suitable to suitable hosts, they shift from sink to source sub-populations. I found evidence for strong source-sink dynamics for the three *Heteropsis* species, as recruited seedlings (72-81%) and ramets (64-74%) were climbing mainly onto non-suitable hosts (Chapter 2) and the non-suitable subpopulations (sinks) had a **λ** <1 when recruitment into these subpopulations was blocked (Chapter 4). The high percentages of seedlings and ramets climbing on non-suitable hosts were most likely due to the high constraints that these two have to find a suitable host, due to the random searching strategy of the seedlings and to the very low density of suitable hosts trees (Chapter 2). Diffendorfer (1998) argued that source-sink population dynamics arises if dispersal is somehow constrained, so that individuals, on average, cannot achieve all the possible dispersal rates between habitats. In the case of *Heteropsis*, the searching method generates the source-sink dynamics. The results emphasize again that **λ**’s of the three *Heteropsis* populations highly depend on the restricted recruitment of seedlings on suitable hosts. This is confirmed by the results on elasticity and loop analyses, which show that the contribution of the subpopulations on suitable hosts was by far the largest in all three species.



Population growth rate - My results indicate that λ's for the three study species were equal or slightly larger than unity and populations would be stable or grow slowly if the vital rates remained unchanged under the studied environmental conditions (*H. oblongifolia*= 1.0446 (1.0025- 1.1230); *H. flexuosa* = 1.0379 (1.0000- 1.2069); *H. macrophylla* = 1.0101 (1.0000- 1.1002), between parentheses are the 95% CI). In general, long-lived species have λ values close to unity (e.g. Nabe-Nielsen 2004; Zotz 2005).

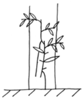
***Vital rates importance to population growth rates* -** I evaluated the relative importance of the vital rates to λ by using elasticity analyses. This method is commonly used to analyze the relative contributions of different life history transitions (e.g. survival, growth) to λ (Franco and Silvertown 2004). I found that the most important vital rate for the λ of the three *Heteropsis* species was survival on suitable hosts while values for sexual reproduction and growth were very low. Similar results were mostly found for woody plants of forest habitats (Caswell 2001; Silvertown et al. 1993; Silvertown & Franco 1993; Pino, Picó & Roa 2007). My three study species reproduced sexually and vegetatively, but, the three modes of vegetative reproduction were far more important than the sexual one. Population dynamics of many species may depend heavily on vegetative reproduction (Eriksson 1992; Silvertown et al. 1993; Mandujano et al 2007; Clark-Tapia et al 2005). Nonetheless, these reproductive modes in the three *Heteropsis* species were relatively unimportant compared to survival. A perturbation analyses that involved complete cessation of clonal reproduction (*K1*, *K2* and *K3*) confirmed the low importance of vegetative reproduction to λ. The population growth of these species did not depend on *K2* (the probability that an individual produces a ramet that descends to the ground and then climbs a host and splits off) and *K3* (the probability that a fallen plant produces shoots that eventually climbed a non-suitable or suitable host and split off). It meant that the strategy of ramet production to search for a new host was in fact not of importance to population growth rate. This suggests that most of the individuals on the non-suitable hosts were 'lost cases' because they did not contribute much to population growth. So far, little or nothing is known about the demographic relevance of vegetative propagation in secondary hemiepiphytes. My study provides a first indication that this form of reproduction is likely more important to population growth compared to sexual reproduction.

HOW LONG DOES IT TAKE TO BECOME A HARVESTABLE ADULT?

Secondary hemiepiphytes produce strong, pliable aerial roots, harvested since ancestral times by indigenous people, to make baskets, fish and terrestrial traps, brooms, and as lashing material for house construction (Whitehead & Godoy 1991, Bennett 1992, Paz y Miño et al. 1995, van Andel 2000, Balcázar & van Andel 2005; Fig 5). In the last decades, these species have become the target of intensive commercial exploitation throughout the Amazon Basin for furniture and handicraft production (Balcázar-Vargas and van Andel 2005, Rodrigues-Ferreira and Bentes-Gama 2005, Wallace and Ferreira 2000). The most common and widely harvested species is *Heteropsis flexuosa* (Hoffman 1997; van Andel 2000a; Wallace & Ferreira 2000; Balcázar-Vargas & van Andel 2005). Other harvestable species of this genus are: *H. macrophylla*, *H. linearis* A.C. Sm, *H. longispathacea* Engl., and *H. spruceana* Schott (Balée, 1994; Paz y Miño et al., 1995; Troy & Harte, 1998, Baluarte & del Castillo Torres 2001, Plowden et al. 2003, Balcázar-Vargas & van Andel 2005). According to the IUCN (IUCN 2012.1; http://www.iucnredlist.org), these species are presently not under threat of extinction. Nevertheless, when indigenous people collect the roots for the craft market, *Heteropsis* species (and other secondary hemiepiphytes with useful aerial roots) generally become scarce around local communities (Balcázar-Vargas and van Andel 2005, Plowden et al. 2003).

Figure 5. A) Field assistant Angel Hichamón (Chutty) making a knot to build a house in the Zafire Biological Station. **B)** Detail of the knot.

Aerial roots of *H. flexuosa* and *macrophylla* can be harvested when the hemiepiphytes reach an upper height of around 10 m on a host (Balcázar-Vargas & van Andel 2005). I have estimated that age at first reproduction (τ) amounts to around 58 years, quite similar as reported for *H. flexuosa* in Guyana (Hoffman 1997). *Heteropsis* is characterized by a long life span (mean lifespan: *H. oblongifolia*= 121, *H. flexuosa*= 37 and *H. macrophylla*= 71 years) and long reproductive life (age at reaching the last category: *H. oblongifolia*= 71, ±SD 86 *H. flexuosa*= 52, ±SD 91 and *H. macrophylla*= 16, ±SD 24 years). Given the very slow growth rates and the high age at harvestable size, there is little scope for cultivation as an alternative to large-scale harvesting of roots from natural populations of *H. flexuosa* and *macrophylla*. Based on the results of this study, it is advised that harvesters prevent killing plants (e.g. by cutting all the adventitious roots) or pulling down the entire plants during root harvesting.

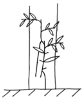


The long time to reach the harvestable size suggests four possible management strategies. First, encourage harvesters to determine the number of *Heteropsis* adults per host in order to harvest roots from different individuals and not all the roots of a single plant. This would reduce the chances of adult mortality due to harvesting. Second, maintain the indigenous tradition of harvesting only one third of the absorbing roots or "bejucos" (Balcázar-Vargas & van Andel 2005), and additionally do not harvest any plant that has less than three roots (Turriago & Balcázar-Vargas unpublished data). Again, this reduces mortality chances, but further studies are required to quantify the effects of different harvesting intensities and determine rates of root mortality and production per year. The third option is to subdivide the extraction area (e.g., an indigenous reserve) in several patches, in which the community establishes root harvesting rotation periods. These periods would be set according to the root production rate per year, of post-harvest plants. Again, such practice should ideally be based on experimental harvesting following this design. Finally, if the indigenous people plan to create a "chagra" (indigenous farming area), I would advise them to cut all the harvestable *Heteropsis* roots. Sustainable harvesting and management of hemiepiphytes in natural populations should be considered as a measure for conservation and management of tropical forests, especially in regions where craft production is the main income for the indigenous and/or settles people, such as the Piaroa people in Resguardo of Cumaral, Vichada, Colombia; (Balcázar-Vargas & van Andel 2005) as many other communities in the Brazilian Amazon (e.g.: Governo do Estado AMAZONAS 2005, Ferreira And Bentes-Gama 2004).

RECOMMENDATIONS FOR FURTHER RESEARCH

FUNDAMENTAL STUDIES

Almost any work on secondary hemiepiphytes will be new knowledge. First and foremost, it is remarkable that in the same family of secondary hemiepiphytes (Araceae) there exist two different strategies to locate a host, skototropism (*Monstera*, Strong & Ray 1975) and random searching (Heteropsis¸ Chapter 2). In the random strategy, most of the *Heteropsis* seedlings that come from the same infrutescence do not mainly climb on their parent host, but on non-suitable hosts' neighbors (Chapter 2), as a consequence most of the seedlings ascend on hosts where no other seedlings of the same species are present (pers. obs.), and therefore avoiding light competition. In contrast, most seedlings of the skototropic species *Monstera gigantea* grow back to their parent host, generating high light competition between the seedlings (Ray 1976). The apparent random searching behavior of *Heteropsis* seedlings and the high proportion of seedlings climbing on non-suitable hosts might avoid competition. The apparent random searching behavior of *Heteropsis* seedlings and the resulting high proportion of climbing seedlings on non-suitable hosts are fascinating and require additional study. Furthermore, it would be very insightful to determine the evolutionary (dis-) advantages of these searching strategies.



Besides the differences in the two searching behaviors, both the seedlings of *Monstera* and *Heteropsis* climb up on non-suitable hosts and as a result they must search for new hosts (Ray 1976, Chapter 2). Vegetative propagation allows *Monstera* and *Heteropsis* to move from a non-suitable host to a suitable one (Ray 1976, 1992, Chapter 2). Further studies are needed to discover what kind of mechanism triggers the production of shoots in *Heteropsis* and other secondary hemiepiphytes. Another complementary and important question would be: Do ramets show the same searching pattern as seedlings? It is expected that *Monstera* ramets show skototropism and that *Heteropsis* ramets show a random searching pattern. To answer what kind of tropism *Heteropsis* seedlings and ramets have, I would replicate the famous Strong and Ray's experiment (Strong and Ray 1975).

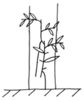
Knab-Vispo et al (2003) found that *Heteropsis* showed a significant preference for certain local forest types and the analysis indicated that this preference was attributable to the abiotic characteristics of these forests rather than their greater density of preferred host tree species or sizes. The researchers took only adult individuals into account, so, they could not infer the consequences of host density on the success that a seedling found host. I found that a very low proportion of recently recruited seedlings climbs on a suitable host from the start. This is probably because the density of suitable hosts in the study area is very low and therefore the chances of finding a suitable host are low (chapter 2). It would be interesting to ask: Could the density of suitable hosts increase the abundance of the studied species or the secondary hemiepiphytes in general?

Finally, all three *Heteropsis* species showed very slow growth with huge variation, while and a considerable percentage did not grow or shrink (Chapter 3). This variation may strongly affect population dynamics (Zuidema & Franco 2001; Zuidema et al. 2009) and if it is maintained over time, persistently fast growers will have a greater chance to reach adult sizes (assuming equal annual mortality risks) and will do so at a younger age than slower growers (Zuidema et al. 2009). At present, it is not known whether growth differences persist over time. Therefore, it will be interesting to determine if such correlation exists and what it would imply for population growth.

APPLIED STUDIES

To design sustainable harvest levels for commercially extracted aerial roots, additional research is needed on secondary hemiepiphytes populations in the Amazon:

1. Inventories of the number of individuals and harvestable roots per hectare at species level across the Amazon should be made. Since more than one individual can be found in a single host, it is important to assess the number of individuals per host and the number of roots per individual per host. Such inventories are important for conservation and management of commercial secondary hemiepiphytes species.



2. Establish permanent plots across the Amazon (or make use of existing ones) to determine vital rates (survival, growth, retrogression, vegetative and sexual reproduction and recruitment) at individual and population levels over time, especially for the commercial species (Chapter 3). This will provide basic ecological information for sustainable harvesting and management and for correlation with climate and other environmental variables.

3. To determine the impacts of different harvest intensities (25%, 50% and 75% of the roots) and different frequencies in natural populations in order to understand individual and population responses to extraction for the useful species.

4. To assess whether the harvest in dry or rainy season have different effects on the adult plants.

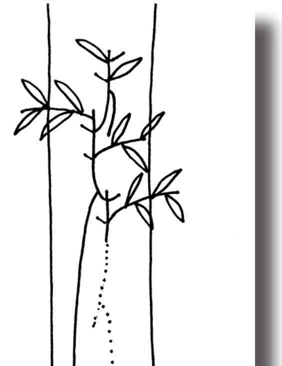
5. Due to the high rate of Amazon forest deforestation, it is very important to assess the effects of forest fragmentation on the *Heteropsis* species.

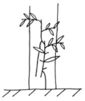
6. Assess the effects of roots harvesting on (inflor-) and infrutescence production and therefore on animal populations that depend on these plants. Several species of primates and birds have been reported as potential consumers, predators and dispersers of *Heteropsis* infrutescences. In primates, Pithecia albicans (Brazil; Peres 1993), Saguinus fuscicollis, Saguinus mystax (Peru, Laurence et al. 2009), Pithecia pithecia, Cebus apella (Suriname, Gregory 2006), and Ateles spp. in central Surinam also resort to a number of reliable non-reproductive plant parts of *Heteropsis* species on a seasonal basis including the aerial root tips and young leaves of *Heteropsis flexuosa* (M. van Roosmalen 1985). Birds like Selenidera maculirostris feed on fruits as well (Galetti, Laps and Pizo 2000). In my research area, a field assistant saw a probably predation event by a Saguinus nigricollis.

7. Identify and test management techniques to reduce negative impacts (e.g.: on $\boldsymbol{\lambda}$, root and inflorescence production) of harvesting on the remaining populations.

Drawing by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Caqueta. In the center Bartoleme Castro weaving a fyke or ‘female’ creel (rigoru)(Huitoto).

Discusión general y resumen





Discusión general y resumen

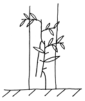
La ecología de hemiepífitas ha sido muy poco estudiada. La historia de vida general de las hemiepífitas primarias ha sido bien descrita, sin embargo las hemiepífitas secundarias han sido hasta ahora ignoradas en los estudios ecológicos (Williams-Linera y Lawton 1995). Lo más notable es la falta de información sobre las tasas vitales y demografía de este ciclo de vida. Esta información es esencial para comprender realmente la ecología, el manejo y la conservación de este grupo que es un componente importante del dosel de los bosques tropicales. En esta tesis, se pretende cubrir algunas de los baches en el conocimiento de la ecología de las hemiepífitas. Estudié tres especies simpátricas de hemiepífitas secundarias en la Amazonia colombiana: *Heteropsis flexuosa* (Kunth) Bunting GS, *H. macrophylla* AC Sm y *H. oblongifolia* Kunth. Primero evalué cómo las plántulas de estas especies encuentran un hospedero (forófito) (capítulo 2) y si estos hospederos son adecuados (es decir, suficientemente altos para que el individuo de *Heteropsis* se pueda reproducir) o no. Luego, describo y explico los patrones de supervivencia, crecimiento, retroceso, reproducción vegetativa y sexual de estas especies, y el efecto del tipo de hospedero (apropiado o no) en estas tasas vitales (capítulo 3). A continuación, analizo la importancia relativa de los dos tipos de hospederos, adecuados (los que son lo suficientemente altos para permitir la reproducción de los individuos de *Heteropsis*) y no adecuados (los que son demasiado bajos) en la demografía de las tres especies ya mencionadas. Por último, estimó la edad a la que las especies de *Heteropsis* alcanzan la reproducción y en la que sus raíces pueden ser cosechadas para ser utilizadas en la producción artesanal (capítulo 4).

El Ciclo De Vida De Una Hemiepífita Secundaria (*Heteropsis*)

La búsqueda de un hospedero - El ciclo de vida de una hemiepífitas secundaria tiene dos fases contrastantes. El primero ocurre después de la germinación y termina cuando la plántula se trepa a un hospedero. Las hemiepífitas secundarias no pueden sostenerse en posición vertical, por lo que necesitan encontrar estructuras adecuadas para trepar y ascender (Putz y Holbrook, 1991). Esto requiere una estrategia de búsqueda eficaz, y lo ideal sería que está la conduzca a un hospedero que pueda sostener a la hemiepífita a lo largo de su vida (Putz 1984).

Estrategia de búsqueda - Una de las preguntas más intrigantes en la ecología de las plantas trepadoras es como enredaderas, lianas y hemiepífitas secundarias encuentran a un hospedero o forófito adecuado (Strong y Ray 1975). En los últimos 130 años, diversas hipótesis se han propuesto. La primera fue hecha por Charles Darwin (1875), que presentó los resultados de sus experimentos en la enredadera *Bignonia capreolata* L., él afirmó que los hospederos fueron encontraron por "afeliotropismo" (crecimiento alejándose de la luz). Desde entonces, varios otros mecanismos han sido sugeridos para lianas y enredaderas, incluyendo geotropismo negativo (crecimiento en contra de la gravedad) por Menninger (1970), la búsqueda aleatoria (Hottes 1933), tigmotropismo (crecimiento en respuesta a contacto mecánico) por Darwin (1875) y Jaffe & Galston (1968) y fototropismo positivo (crecimiento hacia la luz) por Janzen (1969). Strong y Ray (1975) demostraron en un estudio experimental que las plántulas de la hemiepífita secundaria, *Monstera gigantea* (Roxb.) Schott, encuentran un hospedero debido a que estas crecen hacia la silueta que proyecta un árbol, un mecanismo que se denominó escototropismo (Strong & Ray 1975) y Kaufman et al. (1989) denominó fototropismo negativo. Desde entonces, este tema no ha sido estudiado. Yo estudié el comportamiento de búsqueda de hospederos por parte de *Heteropsis* y encontré que los tallos o brotes a menudo mostraron un comportamiento de crecimiento errático: estaban creciendo en direcciones al azar y también cambiaban de rumbo sin señal perceptible (ej., cambio en las condiciones de luz, la obstrucción física). Virtualmente no hubo ninguna plántula que estuviera creciendo en línea recta y a veces se encontró grupos de semillas recientemente germinadas, procedentes de una misma infrutescencia, creciendo en direcciones muy diferentes (Fig. 1). Aunque estas son simplemente observaciones de campo que carecen de mediciones y pruebas estadísticas para determinar si la dirección de crecimiento de plántulas fue de hecho al azar, estas observaciones preliminares sugieren que la búsqueda de hospederos es un proceso aleatorio. Mis observaciones de campo a cerca del crecimiento de las plántulas de *Heteropsis* contrastaron respecto a las halladas o descritas por Strong y Ray (1975) en *Monstera gigantea*. Si el crecimiento de las plántulas de las tres especies de *Heteropsis* fuera regido por el escototropismo, yo hubiera encontrado que la mayoría de las plántulas reclutadas de una misma infrutescencia hubieran crecido en una misma dirección, en lugar de irradiar en diferentes direcciones. Por otra parte, yo habría esperado encontrar que la mayoría de plántulas de *Heteropsis* treparían al hospedero de la madre o árboles grandes y no a los hospederos más pequeños en el bosque, como de hecho se encontró, la mayoría de las plántulas de *Heteropsis* ascendieron a los hospederos más pequeños y no adecuados (Capítulo 2). Aun cuando las plántulas de *Heteropsis* germinaban cerca del árbol huésped de la supuesta planta madre, la mayoría de ellos se subieron a hospederos no adecuados. En contraste, las plántulas de *Monstera* se volvían a trepar al árbol hospedero de su planta madre (Ray 1976).

Encontré una fuerte y formal confirmación del comportamiento de búsqueda aleatoria comparando la distribución del diámetro de los hospederos de las plántulas de *Heteropsis* que acababa de trepar a un hospedero, y la de todos los árboles, palmas y lianas ≥10 cm DAP en las parcelas. Estas distribuciones de diámetros eran muy similares, lo que sugiere que el comportamiento de búsqueda es aleatorio. Por el contrario, cuando se consideraron las distribuciones diamétricas de los hospederos de juveniles y adultos de *Heteropsis*, estas distribuciones difirieron significativamente de las de todos los árboles, palmas y lianas ≥10 cm DAP en las parcelas. Juveniles y adultos de *Heteropsis* se encontraron principalmente en los árboles, palmas y lianas con DAP ≥ 20 cm. Por otra parte, el porcentaje de plántulas presentes en los hospederos de 10-19 cm de DAP fue mayor que el porcentaje de juveniles y adultos en esa categoría. Estos resultados fueron consistentes para las tres especies y parecen sugerir que las plántulas de *Heteropsis* se trepan al azar al hospedero más cercano, y adoptan una estrategia de búsqueda aleatoria en lugar de una dirigida por escototropismo



(capítulo 2). Una vez que las plántulas de *Heteropsis* se trepan en hospederos no aptos, cambian de ellos a través de la reproducción vegetativa.

Figura 1. A). Detalle de una semilla germinada. Tamaño de la semilla: longitud = 1,7 cm * ancho = 1,2 cm. **B)** Plántulas de *Heteropsis flexuosa* después de la germinación. El tallo sin hojas se aleja del punto de germinación. La línea blanca indica la dirección tomada por el tallo de Heteropsis en el suelo del bosque (fotos: M.P. Balcázar-Vargas). Ver página 96.

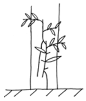
El riesgo de mortalidad en el suelo del bosque - Los tallos sin hojas de plántulas que aún no han trepado experimentan un alto riesgo de mortalidad (72% por año, Capítulo 2 y 3, Fig. 1A y B) causadas por la caída de escombros y el agotamiento de los recursos de la semilla antes de encontrar un hospedero (Ray 1976). Las plántulas que aún no han trepado de *Heteropsis* siguen apegados a sus semillas y sin hojas no pueden realizar la fotosíntesis. Esto las hace vulnerables al agotamiento de las reservas y los límites de su capacidad para recuperarse de los daños, por lo que no pueden sobrevivir por largos períodos. Sin embargo, una plántula que aún no se ha trepado, generalmente sobrevive el tiempo suficiente para alcanzar algún lugar dentro de 1 m de distancia de su lugar de germinación.

El Camino Hacia El Dosel

La segunda fase del ciclo de vida de *Heteropsis* comienza cuando la planta ha encontrado y asciende un hospedero, adhiriéndose a este por medio de raíces adventicias de anclaje (Wilder 1992, Romero 1994; Fig. 2A). Una vez adherida al tronco, la planta produce un segundo tipo de raíces: raíces absorbentes que captan agua y nutrientes del suelo (Fig. 2A). Una vez que estas raíces absorbentes son funcionales, la parte inferior del tallo muere y la planta pierde la conexión inicial con el suelo del bosque y lo que quedaba de la semilla (Fig. 2). A continuación, la planta produce ramas plagiotrópicas (ramas horizontales) y ortotrópicas (ramas verticales) así como más raíces absorbentes. En este proceso, las parte más baja del tallo cénese junto con las raíces más bajas (Putz y Holbrook 1986, Plowden et al. 2003), hasta que la planta alcanza el sotobosque (*H. oblongifolia*), el sub-dosel *H. flexuosa* o el dosel *H. macrophylla* del bosque.

Figura 2. A) Plántulas de *Heteropsis flexuosa* trepadas en un hospedero que aún no poseen raíces absorbentes. **B)** Plántula de *H. flexuosa* trepada en un hospedero con raíces absorbentes y de anclaje (Fotos: M.P. Balcázar-Vargas). Ver página 98.

Figura 3. A) Plántula de *H. flexuosa* trepada en un hospedero que muestra la primera rama plagiotrópica. **B)** Planta de *H. tenuispadix* ascendiendo (especie no incluida en este estudio) que muestra varias ramas plagiotrópicas (Fotos: M.P. Balcázar-Vargas). Ver página 98.



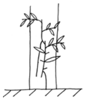
Problemas para llegar al dosel: El hospedero incorrecto! - Probablemente debido a la estrategia de búsqueda aleatoria y a la baja densidad de hospedadores adecuados, la gran mayoría de las plantas de *Heteropsis* trepan en hospederos muy pequeños y no adecuados (81%). Como consecuencia, aquellos individuos no pueden completar su ciclo de vida debido a que la reproducción de las especies de *Heteropsis* está determinada por la altura sobre el hospedero (Fig. 4, Capítulo 2 y 3). Muchos "hospederos" de las especies de estudio fueron efectivamente plantas muertas, hierbas o plántulas de árboles. De hecho, las plántulas de *Heteropsis* se trepan a todo lo que encuentran a su paso, incluso hojas caídas. Este hallazgo es consistente con los resultados de diversos estudios sobre las características de los árboles hospederos de lianas con zarcillo (Putz 1984, Putz y Holbrook 1991, Nabe-Nielsen 2001, Sakai et al. 2002). Como para la mayoría de las lianas (Putz 1984, 2012) y un helecho trepador *Polybotrya pubens* Mart. (Young y León, 1991), los hospedero adecuados son un recurso limitado para las tres especies *Heteropsis*, por lo tanto, las posibilidades de encontrar uno son muy bajas (capítulo 2).

Figura 4. Tallo apical de un hospedero no adecuado denotado por una flecha. Ver página 99.

Una vez en el hospedero incorrecto, ¿qué puede hacer la planta? Como la inmensa mayoría de las plántulas de *Heteropsis* se trepan en hospederos no adecuados, estas tienen que buscar uno nuevo. Propagación clonal a través de la producción de brotes permite que las plantas de *Heteropsis* puedan pasar de un hospedero no apropiado a uno apropiado (Figura 5 B; Capítulo 2). Brotes flageliformes se han interpretado como un mecanismo para superar las condiciones limitantes en la explotación del hábitat de la plantas (Andrade y Mayo 2000). Cada año, entre el 0.6 y el 2.4 por ciento de los individuos de *Heteropsis* producen brotes (ramets) que buscan nuevos hospederos o forófitos, la mayoría de ellos se trepan (de nuevo) en un hospedero no adecuado (capítulo 2). Sin embargo, la proporción de ortets (genets) en huéspedes adecuados incrementó con la producción de clones, porque en el 35 al 46 por ciento de los casos, al menos uno de los ramets subió a un huésped adecuado. Esto significa que estas plantas de larga longevidad probablemente necesitan producir un gran número de ramets, para garantizar que uno de ellos encuentre un hospedero adecuado que permita al ortet reproducirse. Este fenómeno muestra que la búsqueda de hospederos no exclusiva de las plántulas pequeñas. Se trata de un método de búsqueda de ensayo y error a través de la propagación clonal, hasta que la planta sube a un huésped adecuado y alcanza la altura deseada en el (sub-)dosel (*H. flexuosa* y *H. macrophylla*) o el sotobosque (*H. oblongifolia*).

ALCANZANDO EL DOSEL

Las tasas vitales de las especies de Heteropsis - Si bien ha habido avances recientes en la cuantificación de las tasas vitales de lianas, enredaderas, palmas trepadoras (ratanes) y epífitas (ej. Nabe-Nielsen 2004, Zotz 2005, Gilbert et al. 2006, Kouassi et al. 2008, Binh 2009), ese conocimiento no se tiene de las hemiepífitas (Williams-Linera y Lawton 1995).

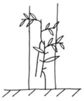


Yo proporciono ideas básicas a cerca de las tasas vitales (supervivencia, crecimiento, propagación vegetativa y reproducción sexual) de tres especies del género *Heteropsis* y exploro los factores que rigen su funcionamiento. A mi entender, este es el primer estudio de este tipo que proporciona información sobre la ecología de hemiepífitas secundarias. Características generales de las especies de estudio se muestran en la Tabla 1.

Supervivencia- Una vez que las tres especies de *Heteropsis* se subieron a un hospedero la probabilidad de supervivencia aumentó enormemente (94-85%, Tabla 1), un fenómeno que también se observa en lianas (Nabe-Nielsen 2004, Gerwing 2004). *Heteropsis* (al igual que otras hemiepífitas secundarias) crecen muy pegadas al tronco (Fig. 2), lo que puede reducir el daño y la mortalidad debido a la caída de escombros (Ray 1976).

Crecimiento - Yo tenía dos hipótesis sobre la tasas de crecimiento en altura, la primera estaba relacionado con que tan rápido pueden crecer las plantas de *Heteropsis* y la segunda con cómo cambian las tasas de crecimiento con el tamaño del individuo. Mi primera hipótesis sugería que estas plantas deben ser capaces de alcanzar altas tasas de crecimiento en altura, tal como las lianas las y enredaderas, debido a que: 1) los tallos tienen sólo una función de soporte limitado y la biomasa asignada a ellos puede ser invertida en la extensión y no en la rigidez y robustez del tallo (Bell et al 1988; Darwin 1867; Putz 1984, den Dubbelden y Verburg 1996). 2) El hábitat de las epífitas es muy dinámico, por lo tanto, se podría esperar que estas plantas responden a esta presión selectiva, mostrando altas tasas de crecimiento, una madurez reproductiva precoz y una producción de semilla abundante (Benzing 1978). 3) Las hemiepífitas secundarias poseen raíces absorbentes que les permiten estar conectadas al suelo y absorber agua y nutrientes de forma continua (Croat 1981). Mi segunda hipótesis por lo tanto esperaba que las tasas de crecimiento aumentaran conforme a que las plantas ascendieran en altura hacia el dosel. Como las plantas a medida que asciende en altura poseen un mayor número y más grueso de raíces absorbentes, ramas plagiotrópicas y un mayor acceso a la luz, ellas pueden obtener más agua y nutrientes y por lo tanto fotosíntetizar más. Sin embargo, mis resultados no dieron lugar a la adopción de estas hipótesis: las tres especies de *Heteropsis* crecieron muy lentamente en altura (aproximadamente 2 - 8 cm/año), con un número importante de individuos (hasta 62%) que no crecieron en absoluto o que disminuyeron en altura en un período de dos años (Capítulo 3, Tabla 1) y el aumento en la tasa de crecimiento se produjo, pero no era tan alto como yo esperaba. Estos resultados también contrastan fuertemente con las tasas de crecimiento de los ratanes y lianas (Bøgh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, 1990b, Schnitzer 2005). El lento crecimiento de las hemiepífitas secundarias posiblemente se explica por la limitada cantidad de nutrientes y agua que pueden ser absorbidos por las raíces absorbentes, pero esto sigue siendo especulativo.

Encontré que la cantidad de luz y el número de raíces afecta en cierta medida positivamente la tasa de crecimiento de *Heteropsis macrophylla*. Relaciones similares entre el crecimiento y la luz se han encontrado en lianas tolerantes a la sombra como *Machaerium cuspidatum* Kuhlm. & Hoehne y *Connarus turczaninowii* Triana (Nabe-Nielsen 2002, Aide y Zimmerman 1990), y en seis especies de ratanes (Binh 2009, Bong 1996). Aunque el

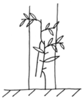


crecimiento en altura de *Heteropsis* es ciertamente limitado por la luz, la escasez de agua y nutrientes pueden jugar un papel adicional, sugerido por el efecto del número de raíces absorbentes en la tasa de crecimiento en altura. Nuevos estudios muestran que a medida que las plantas adultas de *Heteropsis* ascienden en altura en un hospedero, tanto el número como el grosor de las raíces absorbente aumenta. Como resultado, la eficiencia hidráulica mejora, es decir, la cantidad de agua que puede pasar a través de una cierta estructura (raíz, tallo, pecíolo) por unidad de tiempo y gradiente de presión (Martínez-Vilalta y Piñol 2003, Gil-Pelegrín et al. 2005, Burgess et al. 2006). En otras palabras, a medida que las raíces aumentan su diámetro, ellas son capaces de transportar más agua y por lo tanto mantener una mayor cantidad de biomasa (Turriago *conv. pers.*).

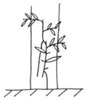
Una gran proporción de plántulas que pertenecen al género *Heteropsis* y a las lianas tendriladas se trepan a hospederos no aptos donde no pueden completar su ciclo de vida (Putz 1984, Putz y Holbrook 1991, Nabe-Nielsen 2001, Sakai et al. 2002, Balcázar-Vargas et al. 2012). Dado que los individuos carecen de suficiente apoyo vertical, ellos tienden a invertir más recursos en la producción de brotes que se mueven hacia abajo en busca de nuevos forófitos. Por lo tanto, yo esperaba que las plantas en hospederos adecuados crecieran más rápido en altura que las plantas en hospederos no adecuados. Sin embargo, no hubo diferencias significativas en las tasas de crecimiento en altura superior entre plantas en estos dos tipos de hospederos, en ninguna de las tres especies. En contraste, en lianas se ha encontrado que crecen dos a siete veces más rápido cuando encuentran soportes adecuados, proporcionados experimentalmente (Putz 1984). Para resumir, la idoneidad del hospedero no afectó la supervivencia y el crecimiento de las tres especies *Heteropsis* en el corto plazo.

Tabla 1. Comparaciones de las tres especies de *Heteropsis* estudiadas. **Plántulas**: *H. oblongifolia*: individuos con una altura superior de 0.01 a 0.50 y de *H. flexuosa* y *macrophylla* de 0.01 a 1.00 m en hospederos adecuados y no adecuados. **Juveniles**: *H. oblongifolia*: individuos con alturas superiores entre 0.51 y 1.49 y *H. flexuosa* y *macrophylla* entre 1.01 y 9.99 m en hospederos adecuados y no adecuados. **Adultos** *H. oblongifolia*: individuos con una alturas ≥ 1.5 y *H. flexuosa* y *macrophylla* ≥ 10 m en hospederos adecuados. Se dan los valores medios de abundancia. La tasa promedio de crecimiento en altura incluye individuos con crecimiento negativo y positivo y aquellos que no crecieron. La tasa promedio de crecimiento positivo en altura incluyen solamente los individuos con un crecimiento en altura positiva. La importancia de las etapas de la vida y las tasas vitales se basa en el análisis de la elasticidad de los modelos matriciales de poblacionales (capítulo 4).

Especies		***H. oblongifolia***	***H. flexuosa***	***H. macrophylla***
Características generales				
Altura máxima del adulto	[m]	14	25	35
Tamaño mínimo de reproducción	[m]	≥ 1.5	≥ 10	≥ 10
Reproducción		Semilla & vegetativo	Semilla & vegetativo	Semilla & vegetativo



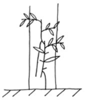
Species	*H. oblongifolia*	*H. flexuosa*	*H. macrophylla*
Abundancia total [ha-1]	125	569	102
Tasa promedio de crecimiento en altura [m por año-1]	0.0208	0.0768	0.0797
Tasa máxima de crecimiento en altura [m por año-1]	0.8051	2.7830	2.9308
Tasa promedio de crecimiento positivo en altura [m por año-1]	0.1333	0.1953	0.2032
Plántulas, tasa promedio de crecimiento positivo en altura [m por año-1]	0.0444	0.0424	0.0468
Juveniles, tasa promedio de crecimiento positivo en altura [m por año-1]	0.1963	0.2626	0.2478
Adultos, tasa promedio de crecimiento positivo en altura [m por año-1]	0.2938	0.5720	0.7141
Abundancia de individuos caídos [ha-1]	9	9	4
Abundancia de individuos en hospederos no apropiados [ha-1]	36	360	63
Abundancia de individuos en hospederos apropiados [ha-1]	80	201	36
Abundancia de plántulas [ha-1]	65	455	63
Abundancia de adultos o individuos cosechables [ha-1]*	17	23	2
Porcentaje de individuos reclutados en hospederos no apropiados [% año-1]	85	70	73
Porcentaje de individuos reclutados en hospederos apropiados [% año-1]	15	30	27
Estrategia de regeneración	Tolerante a la sombra	Tolerante a la sombra	Tolerante a la sombra
Dinámica de poblaciones			
Tasa de crecimiento de la población (λ)	1.0446	1.0379	1.0101
Intervalo de confianza (Bootstrap 95%)	1.0025-1.1230	1.0000-1.2069	1.0000-1.1002
Sobrevivencia de plántulas que aun no se han trepado [% año-1]	-	28	28



Species	*H. oblongifolia*	*H. flexuosa*	*H. macrophylla*
Sobrevivencia de plántulas trepadas [% año-1]	90.9	83.7	95.1
Sobrevivencia de adultos [% año-1]	99.5	99.9	95.6
Sobrevivencia de individuos caídos [% año-1]	72.4	67.9	78.6
Porcentaje de plantas que no crecieron o que redujeron su tamaño durante dos años [%]	62	44	31
Porcentaje de adultos reproductivos [%]	10.7	35.4	49.1
Estado más importante	Plantas en hospederos apropiados	Plantas en hospederos apropiados	Plantas en hospederos apropiados
Estados de vida más importantes [altura superior en m]	> 5	> 7	> 20
Tasas vitales más importantes	Sobre-vivencia en hospederos apropiados	Sobre-vivencia en hospederos apropiados	Sobre-vivencia en hospederos apropiados
Esperanza de vida media [años]	121	37	71
Esperanza de vida media [años]	28	58	58

*: *Heteropsis flexuosa* y *macrophylla* pueden ser cosechadas a partir de los 10 m de altura superior sobre un hospedero. *H. oblongifolia* no es una especie cosechable y se empieza a reproducirse a los 1.5 m de altura sobre un hospedero.

Fecundidad - Al igual que muchas otras especies, las especies del género *Heteropsis* deben alcanzar un umbral de tamaño antes de empezar a reproducirse (Gross 1981, Klinkhamer et al. 1987, Ohlson 1988, Primack y Hall 1990, Méndez y Obeso 1993.). Las especies del (sub-)dosel: *H. flexuosa* y *H. macrophylla* empiezan a reproducirse o de producir inflorescencias a partir de los ≥ 10 m, mientras que *H. oblongifolia* a partir de ≥ 1,5 m (Capítulo 2, Tabla 1). Para las especies de dosel, la probabilidad de producir inflorescencia aumentó con el número de ramas plagiotrópicas y la altura superior. De este modo, plantas con la misma altura superior pero con un mayor número de ramas podrían producir más inflorescencias, ya que las inflorescencias sólo se produce en las ramas plagiotrópicas. Por otra parte, el número de las inflorescencias producidas por planta no fue significativamente relacionado con la altura superior en dos de las tres especies.

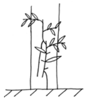


Una Vez En El Dosel, Los Problemas No Se Terminan

Las epífitas y hemiepífitas ocupan un sustrato muy dinámico. El sustrato puede ir aumentando gradualmente en altura a medida que crece el hospedero o ser destruido de repente cuando este se cae (Zotz 1998). Una vez que el hospedero se ha caído, la supervivencia en el suelo del bosque suele ser breve para las epífitas (Matelson et al. 1993). Por el contrario, los individuos de *Heteropsis* pueden sobrevivir después de caer desde o con su hospedero: hasta un 78% de estos individuos caídos sobrevive en el suelo, no sé específicamente cuántos años una planta de *Heteropsis* pueden vivir en el suelo, pero yo encontré algunos individuos algunos centímetros por debajo la capa de hojarasca produciendo ramets de modo continuo, lo que significa que algunos de ellos son capaces de vivir durante años en el suelo. Como tales, los individuos caídos de *Heteropsis* se comportan parecido a los ratanes (Putz 1990a) y a las lianas (90% de supervivencia; Putz 1984). Después de la caída, las tres especies de *Heteropsis* mostraron una alta producción de brotes, especialmente en *H. oblongifolia* (46%). Aunque las epífitas caídas no mueren inmediatamente, sus posibilidades de volver a producir progenie es prácticamente cero (Hietz et al. 2002). Las lianas, sin embargo, brotan con fuerza tras caer en los bosques naturales y de tala selectiva (Putz 1984, Appanah y Putz 1984). A este respecto, las especies estudiadas de *Heteropsis* se comportan más como lianas. Esto tiene consecuencias en su esperanza de vida, ya que la esperanza de vida no está limitada por el hospedero. Individuos hemiepífitos (genets) que tienen la capacidad de sobrevivir a la caída de su hospedero y producir nuevas brotes (ramets) que trepan a los nuevos hospederos, serán capaces de sobrevivir a la muerte de su forófito. Como conclusión, las especies de *Heteropsis* parecen tener una alta resiliencia a la caída de sus hospederos, unas elevadas tasas de supervivencia anual (Tabla 1) y una alta producción de brotes después de caer, lo que sugiere que los genets de estas especies pueden alcanzar avanzadas edades. En efecto, las estimaciones de edad basadas en modelos de matriz muestran que los ramets de *Heteropsis* se caracterizan por una esperanza de vida de 37 a 121 años (Tabla 1), lo que sugiere que este será considerablemente mayor para los genets.

Demografía De Las Tres Especies De *Heteropsis*.

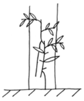
En la sección anterior, mostré que la mayoría de las tasas vitales no fueron diferentes entre mis tres especie de estudio o entre los dos tipos de forófitos. Sin embargo, como muchas plántulas recién reclutadas se trepan a hospederos no adecuados y solo pueden acceder a hospederos adecuados a través de la reproducción clonal, es posible que esta vía a través del ciclo de vida en hospederos no adecuados contribuye sustancialmente a la tasa de crecimiento de la población (λ). Por consiguiente, en esta sección, yo evalúo las consecuencias demográficas de la idoneidad de los hospederos basada en tres análisis diferentes: elasticidad (de Kroon et al. 1986, 2000, Caswell 2001), análisis de ciclo de vida (‘loop analysis’ en inglés, Güneralp 2007) y análisis de la dinámica de fuente y sumidero (Pulliam 1988; Hanski 1999). Este es un tema que no ha sido estudiado hasta ahora en



ninguna planta trepadora (lianas, ratanes o hemiepífitas secundarias).

El significado de la idoneidad del hospedero - Para evaluar el papel de los tipos de hospederos (no apto y adecuado) en λ, yo realicé análisis de elasticidad y de ciclo. Según estos análisis, las plantas en hospederos adecuados tienen la mayor relevancia para λ. Por lo tanto, la pequeña proporción de plántulas que se trepan a hospederos adecuados (19 - 28%) y sobreviven hasta que llegan a un estado de reproducción, contribuyen más a λ que la gran proporción de plántulas que se trepan a hospederos no aptos. Las poblaciones de las tres especies de *Heteropsis* crecen, a pesar de la estrategia aleatoria para encontrar un hospedero, la alta mortalidad de plántulas en el suelo y la muy baja densidad de hospedadores adecuados que finalmente se traduce en niveles muy bajos de reclutamiento en este tipo de hospedadores (Capítulo 2 y 3). La clave para el mantenimiento de estas poblaciones es probablemente la larga esperanza de vida reproductiva de estas especies.

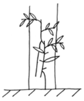
Dinámica de fuentes y sumideros - Una característica común de todos los modelos de fuente-sumidero es que las diferencias entre los hábitats son extremas. En el hábitat de alta calidad (la fuente), los individuos tienen un fitness medio >1 y esta población, en promedio, tiene un $\lambda \geq 1$. El hábitat de menor calidad (el sumidero) es tan pobre que los individuos tienen un fitness promedio <1 y en la ausencia de inmigración, la población decrece hacia la extinción (Diffendorfe 1998, Pulliam 1988; Hanski 1999). En equilibrio demográfico (o durante largos períodos de tiempo), modelos de fuente-sumidero predicen que el hábitat de fuente es un exportador neto de individuos, mientras que el hábitat sumidero es un importador neto. Adaptando la teoría de la dinámica de fuente-sumidero a las hemiepífitas secundarias, los individuos en hospederos aptos y no adecuados pueden ser vistos como sub-poblaciones separadas. Para efectos prácticos, yo uso aquí el término sub-poblaciones, para definir el conjunto de plantas que trepan ya sea en hospederos no adecuados o apropiados. Los individuos en hospederos aptos actúan como la sub-población fuente, ya que son capaces de reproducirse y producir descendencia, mientras que los no adecuados actúan como sub-poblaciones sumidero porque se “extinguirían” en ausencia de la reproducción que proviene de la sub-población fuente en hospederos adecuados. En consecuencia, cuando los individuos se mueven de hospederos no adecuados a aptos, cambian de sub-poblaciones sumidero a fuente. Encontré fuertes evidencias de una dinámica fuente-sumidero para las tres especies de *Heteropsis*, debido a que plántulas reclutadas (72-81%) y brotes vegetativos (64-74%) se trepan principalmente a forófitos no adecuados (Capítulo 2) y las sub-poblaciones en no adecuados (sumideros) tuvieron λ's <1 cuando el reclutamiento en estas sub-poblaciones fue bloqueado (capítulo 4). Los altos porcentajes de plántulas y brotes vegetativos trepándose a hospederos no adecuados se debieron muy probablemente a las altas limitaciones que estos dos tienen para encontrar un hospedero adecuado, debido a la estrategia de búsqueda aleatoria de las plántulas y de la muy baja densidad de árboles hospederos adecuados (capítulo 2). Diffendorfer (1998) argumenta que la dinámica fuente-sumidero de una población surge si la dispersión es de alguna manera limitada, por lo que los individuos, en promedio, no puede alcanzar todas las posibles tasas de dispersión entre hábitats. En el caso de *Heteropsis*, el método de búsqueda de hospederos genera la dinámica fuente-sumidero. Los resultados ponen



de relieve una vez más que las λ's de las tres poblaciones de *Heteropsis* dependen en gran medida del reclutamiento de plántulas restringidas a hospederos adecuados. Esto lo confirman los resultados de los análisis de elasticidad y ciclo de vida, que muestran que la contribución de las sub-poblaciones en hospederos adecuados fue de lejos la más grande de las tres especies.

Tasa de crecimiento de la población - Mis resultados indican que las tasas de crecimiento (λ) para las tres especies fueron iguales o ligeramente mayores que la unidad y las poblaciones estarían estables o creciendo lentamente si las tasas vitales se mantuvieran sin cambios en las condiciones ambientales estudiadas (*H. oblongifolia* = 1.0446 (1.0025 a 1.1230); *H. flexuosa* = 1.0379 (1.0000 a 1.2069); *H. macrophylla* = 1.0101 (1.0000-1.1002), entre paréntesis los IC del 95%). En general, las especies de larga vida tienen valores de λ cercanos a la unidad (por ejemplo, Nabe-Nielsen 2004; Zotz 2005).

***Las importancia de las tasas vitales para el crecimiento de la población* -** yo evalué la importancia relativa de las tasas vitales para λ mediante análisis de elasticidad. Este método se utiliza comúnmente para analizar las contribuciones relativas de las diferentes transiciones de la historia de vida (por ejemplo, supervivencia, crecimiento) a λ (Franco y Silvertown 2004). Yo encontré que la tasa vital más importante para los λ de las tres especies de *Heteropsis* fue la supervivencia en hospederos adecuados, mientras que los valores de la reproducción sexual y el crecimiento fueron muy bajos. Resultados similares han sido reportados en su mayoría para las plantas leñosas de bosques (Caswell 2001; Silvertown et al. 1993; Silvertown y Franco 1993; Pino, Picó y Roa 2007). Mis tres especies estudiadas se reproducen sexual y vegetativamente, pero las tres modalidades de reproducción vegetativa, fueron mucho más importante que la sexual. La dinámica poblacional de muchas especies puede depender en gran medida de la reproducción vegetativa (Eriksson 1992; Silvertown et al. 1993; Mandujano et al. 2007; Clark-Tapia et al. 2005). Sin embargo, estos modos de reproducción en las tres especies de *Heteropsis* fueron relativamente poco importantes en comparación con la supervivencia. Un análisis de perturbación en donde se eliminó por completo los tres tipos de reproducción clonal (*K1*, *K2* y *K3*) confirmaron la poca importancia de la reproducción vegetativa a λ. El crecimiento de la población de estas especies no dependió de *K2* (la probabilidad de que un individuo produce un ramet que desciende al suelo del bosque y se trepa en un hospedero y se separa) y *K3* (la probabilidad de que una planta caída produce brotes que con el tiempo se trepan a un hospedero no adecuado o apropiado y se separa). Eso significaba de hecho, que la estrategia de producción de ramets para buscar un nuevo hospedero, no es de importancia para la tasa de crecimiento poblacional. En conclusión, la mayoría de los individuos en hospederos no adecuados son "casos perdidos" porque no contribuyen mucho al crecimiento demográfico. Hasta ahora, poco o nada se sabe de la importancia demográfica de propagación vegetativa en hemiepífitas secundarias. Mi estudio proporciona una primera indicación de que esta forma de reproducción es probablemente más importante para el crecimiento de la población que la reproducción sexual.



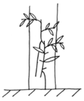
¿Cuánto tiempo necesita para llegar a ser un adulto cosechable?

Las hemiepífitas secundarias producen raíces aéreas fuertes y flexibles, que han sido cosechadas desde tiempos ancestrales por los pueblos indígenas, para hacer cestas, nasas, trampas, escobas, y como amarres para construcción de viviendas (Whitehead & Godoy 1991, Bennett 1992, Paz y Miño et al. 1995, van Andel 2000, Balcázar & van Andel 2005; Fig. 5). En las últimas décadas, estas especies se han convertido en el blanco de la explotación intensiva comercial a lo largo de la cuenca del Amazonas para la producción de muebles y artesanías (Balcázar-Vargas y van Andel 2005, Rodrigues Ferreira y Bentes Gama-2005, Wallace y Ferreira 2000). La especie más común y ampliamente cosechada es *Heteropsis flexuosa* (Hoffman 1997; van Andel 2000a; Wallace & Ferreira 2000; Balcázar-Vargas & van Andel 2005). Otras especies cosechables de este género son: *H. macrophylla*, *H. linearis* AC Sm, *H. longispathacea* Engl, y *H. spruceana* Schott (Balée 1994, Paz y Miño et al. 1995, Troy & Harte 1998, Baluarte. y del Castillo Torres 2001, Plowden et al. 2003, Balcázar-Vargas & van Andel 2005). Según la UICN (UICN 2012,1; http://www.iucnredlist.org), estas especies no están actualmente bajo amenaza de extinción. Sin embargo, cuando los indígenas cosechan las raíces para el mercado de artesanías, las especies de *Heteropsis* (y otras hemiepífitas secundarias con raíces aéreas útiles) generalmente escasean en torno a las comunidades locales (Balcázar-Vargas y van Andel 2005, Plowden et al. 2003).

Figura 5. A) Asistente Ángel Hichamón (Chutty) haciendo un nudo para construir una casa en la Estación Biológica Zafire. **B)** Detalle del nudo. Ver página 106.

Las raíces aéreas de *H. flexuosa* y *macrophylla* son cosechadas cuando las hemiepífitas alcanzan una altura superior a los 10 m en un hospedero (Balcázar-Vargas & van Andel 2005). He calculado que la edad de la primera reproducción (τ) se produce alrededor de los 58 años, muy similar a la reportada para *H. flexuosa* en Guyana (Hoffman, 1997). *Heteropsis* se caracteriza por una gran longevidad (esperanza de vida media: *H. oblongifolia* = 121, *H. flexuosa* = 37 y *H. macrophylla* = 71 años) y una larga vida reproductiva (edad al llegar a la última categoría: *H. oblongifolia*= 71, ± SD 86 *H. flexuosa*= 52, SD ± 91 y *H. macrophylla*= 16, SD ± 24 años). Teniendo en cuenta las tasas de crecimiento muy lento y la edad mínima para alcanzar un tamaño comercial de *H. flexuosa* y *macrophylla*, hay muy pocas probabilidades para que el cultivo de estas especies sea considerado como una alternativa a la cosecha de raíces de poblaciones silvestres. Con base en los resultados de este estudio, se aconseja que los recolectores eviten matar a las plantas (por ejemplo, mediante la recolección de todas las raíces adventicias) o tirando abajo las plantas enteras durante la cosecha raíz.

El largo tiempo que requieren están plantas para alcanzar el tamaño comercial sugiere cuatro posibles estrategias de gestión o manejo. En primer lugar, motivar a los cosechadores para determinar el número de adultos de *Heteropsis* por hospedero con el fin de cosechar raíces de diferentes individuos y no todas las raíces de una sola planta. Esto reduciría la mortalidad de adultos debido a la cosecha. En segundo lugar, mantener la tradición indígena de la cosecha, sólo un tercio de las raíces absorbentes o “bejucos” (Balcázar-Vargas & van Andel 2005)



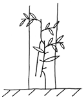
y además no cosechar ninguna planta que tenga menos de tres raíces (Turriago y Balcázar-Vargas, datos no publicados). De nuevo, esto reduce las posibilidades de mortalidad, pero se necesitan más estudios para cuantificar los efectos de las diferentes intensidades de cosecha y determinar las tasas de mortalidad y la producción anual de las raíces. La tercera opción consiste en subdividir la zona de extracción (ej. una reserva indígena) en varios parches, en la que la comunidad establece los períodos de rotación de cosecha. Estos plazos se establecerían de acuerdo a la tasa de producción de raíces por año de las plantas después de la cosecha. Una vez más, esta práctica sería ideal si se basa en los resultados de un diseño experimental siguiendo este diseño. Por último, si los indígenas planean crear un “chagra” (zona agrícola indígena), yo les aconsejaría que cortaran todas las raíces cosechables de *Heteropsis*. Aprovechamiento y gestión sostenibles de las poblaciones naturales de hemiepífitas debe ser considerado como una medida de conservación y ordenación de los bosques tropicales, especialmente en las regiones donde la producción artesanal es la principal fuente de ingresos para las comunidades indígenas y / o de “colonos”, como el pueblo indígena Piaroa del Resguardo de Cumaral, Vichada, Colombia, (Balcázar-Vargas & van Andel 2005), o como muchas otras comunidades en la Amazonia brasileña (por ejemplo: Governo do Estado AMAZONAS 2005, Ferreira y Bentes-Gama 2004).

Recomendaciones Para Futuras Investigaciones

Estudios Fundamentales

Casi cualquier trabajo en hemiepífitas secundarios será un nuevo aporte. En primer lugar, hay que destacar que en la misma familia de hemiepífitas secundarias (Araceae), existen dos estrategias diferentes para localizar un hospedero, escototropismo (*Monstera*, Strong & Ray 1975) y búsqueda aleatoria (Heteropsis¸ Capítulo 2). En la estrategia aleatoria, la mayoría de las plántulas de *Heteropsis* que provienen de la misma infrutescencia no se trepan en el hospedero de su planta madre, pero si en hospedadores vecinos no adecuados (Capítulo 2), como consecuencia la mayoría de las plántulas ascienden en hospederos donde no están presentes otras plántulas de su misma especie (obs. pers.), y por lo tanto evitan la competencia por luz. En contraste, la mayoría de las plántulas de la especie escototrópica *Monstera gigantea*, crecer de vuelta a su hospedero madre, lo que genera una alta competencia por luz entre las plántulas (Ray 1976). El aparente comportamiento de búsqueda aleatoria de las plántulas de *Heteropsis* y la alta proporción de plántulas que se trepan en hospederos no adecuados podría estar evitando este tipo de competencia. Este tipo de comportamiento de búsqueda aleatoria y la alta proporción de plántulas que se trepan en hospederos no adecuados son fascinantes y requieren de estudios adicionales. Por otra parte, sería muy revelador determinar las (des)ventajas evolutivas de estas estrategias de búsqueda.

A pesar de las diferencias en los dos comportamientos de búsqueda, tanto las plantas de *Monstera* y *Heteropsis* se trepan en hospederos no adecuadas y como consecuencia



deben buscar nuevos hospederos (Ray 1976, capítulo 2). La propagación vegetativa permite a las plantas de *Monstera* y *Heteropsis* pasar de un hospedero no apto a uno adecuado (Ray 1976, 1992, capítulo 2). Se necesitan más estudios para determinar qué tipo de mecanismo(s) desencadena(n) la producción de brotes secundarios en *Heteropsis* y otras hemiepífitas. Otra pregunta complementaria e importante sería: ¿muestran los brotes secundarios (ramets) el mismo patrón de búsqueda que las plántulas? Se espera que los ramets de *Monstera* muestren escototropismo y los ramets de *Heteropsis* un patrón de búsqueda aleatoria. Para responder qué tipo de tropismo tienen las plántulas y los brotes vegetativos de *Heteropsis*, me gustaría replicar el famoso experimento de Strong y Ray publicado en la revista Nature (Strong y Ray 1975).

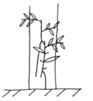
Knab-Vispo et al. (2003) encontraron que las plantas de *Heteropsis* mostraron una preferencia significativa por ciertos tipos de bosques y el análisis indicó que esta preferencia se debió a las características abióticas de estos bosques en lugar de una mayor densidad de árboles hospederos de ciertas especies o tamaños preferidos. Los investigadores sólo tomaron en cuenta a individuos adultos, por lo tanto, ellos no pudieron deducir las consecuencias de la densidad de los hospederos en el éxito que una plántula recién germinada puede tener para encontrar un hospedero. Yo encontré que una muy baja proporción de plántulas recién germinadas se sube por primera vez a un hospedero adecuado. Esto es probablemente debido a que en el área de estudio la densidad de hospedadores adecuados es muy baja, por lo que las posibilidades de encontrar un hospedero adecuado son bajas (capítulo 2). Sería interesante preguntarse: ¿Podría la densidad de hospedadores adecuados incrementar la abundancia de las especies estudiadas o de los hemiepífitas secundarios en general?

Por último, las tres especies de *Heteropsis* mostraron un crecimiento muy lento, con una gran variación, mientras que un porcentaje considerable no creció o se redujo (capítulo 3). Esta variación puede afectar fuertemente la dinámica de la población (Zuidema & Franco 2001;. Zuidema et al. 2009), y si se mantiene en el tiempo, los individuos que persisten en un crecimiento rápido tendrán una mayor oportunidad de alcanzar un estado adulto (suponiendo iguales riesgos de mortalidad anuales) y alcanzaran a ser adultos a una edad mucho menor que los que crecen más lento (Zuidema et al. 2009). En la actualidad, no se sabe si las diferencias de crecimiento persisten en el tiempo. Por lo tanto, sería interesante determinar si tal correlación existe y lo que ello implicaría para el crecimiento de la población.

ESTUDIOS APLICADOS

Para diseñar un plan de manejo sobre los niveles de explotación sostenibles para el comercio de raíces aéreas de *Heteropsis* u otras hemiepífitas secundarias, se necesita investigación adicional:

1. Realizar inventarios de la cantidad de individuos y raíces aprovechables por hectárea a nivel de especie en la Amazonía. Debido que en cada hospedero se pueden encontrar más de un individuo, es importante evaluar el número de



individuos por hospedero y el número de raíces por individuo por hospedero. Estos inventarios son importantes para la conservación y la gestión de especies comerciales de hemiepífitas secundarias.

2. Establecer parcelas permanentes en toda la Amazonía (o hacer uso de las existentes) para determinar las tasas vitales (supervivencia, crecimiento, retroceso, reproducción vegetativa y sexual y reclutamiento) a nivel de individuo y de la población a través del tiempo, especialmente para las especies comerciales (capítulo 2). Esto proporcionará información ecológica básica para el aprovechamiento sostenible y la gestión y la correlación con el clima y otras variables ambientales.

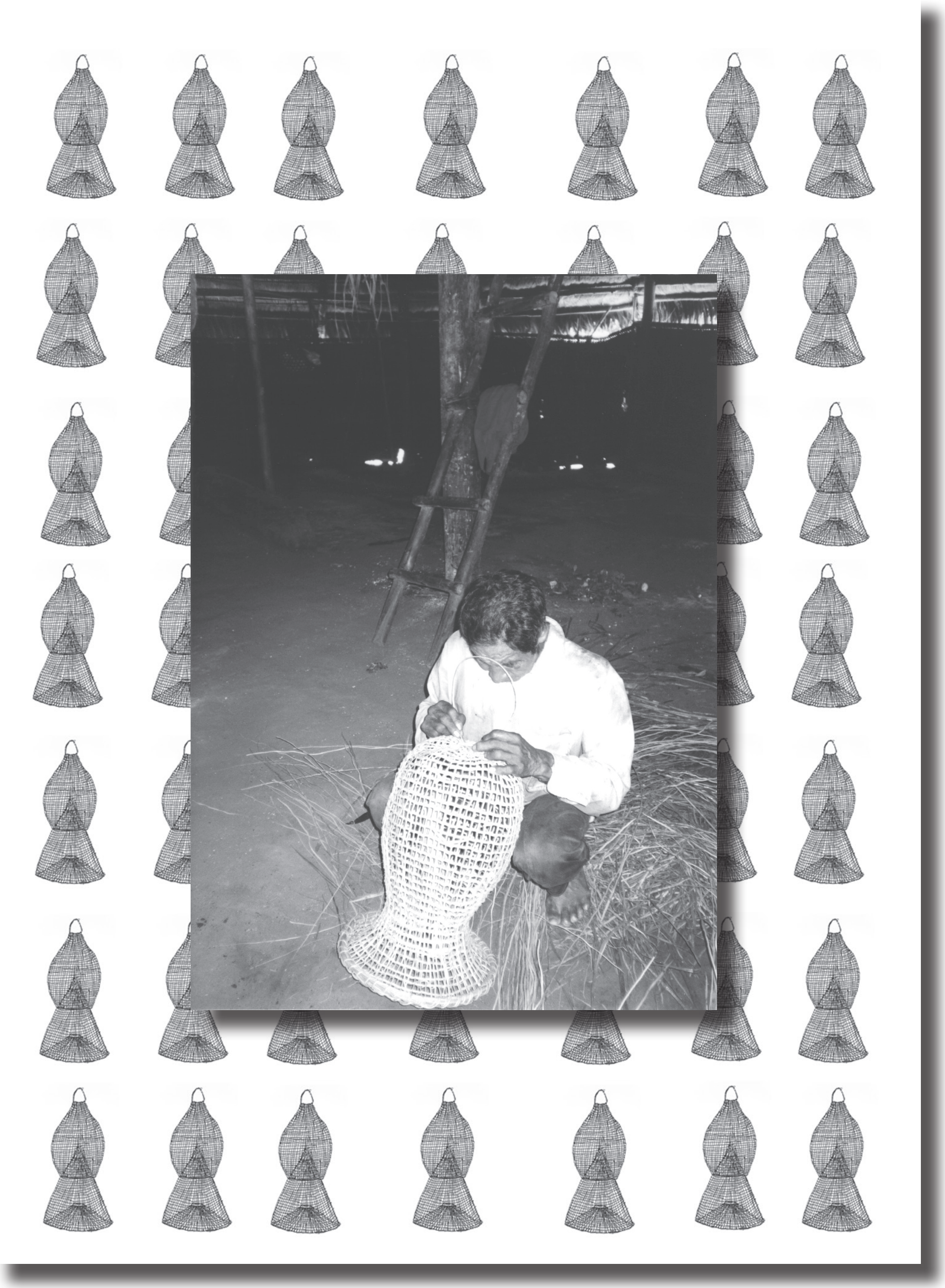
3. Determinar los efectos de las diferentes intensidades de cosecha (25, 50 y 75% de las raíces) y frecuencias, en poblaciones naturales con el fin de entender las respuestas a nivel del individuo y la población de la extracción de raíces de las especies útiles.

4. Evaluar si la cosecha tiene diferentes efectos en las plantas adultas en la estación seca o lluviosa.

5. Debido a las altas tasas de deforestación de los bosques Amazónicos, es muy importante evaluar los efectos de la fragmentación sobre las especies *Heteropsis*.

6. Evaluar los efectos de la cosecha de las raíces en la producción de (inflor-) e infrutescencia y por tanto en las poblaciones de animales que dependen de estas plantas. Varias especies de primates y aves han sido reportadas como potenciales consumidores, predadores y dispersores de infrutescences de *Heteropsis*. En los primates, *Pithecia albicans* (Brasil, Peres 1993), *Saguinus fuscicollis*, *Saguinus mystax* (Perú, Laurence et al. 2009), *Pithecia pithecia*, *Cebus apella* (Surinam, Gregory 2006), y *Ateles* spp. (Surinam, M. van Roosmalen 1985) también consumen partes no reproductivas de *Heteropsis* en algunas temporadas, incluyendo las puntas de las raíces aéreas y hojas jóvenes de *Heteropsis flexuosa*. Aves como Selenidera maculirostris se alimenta también de las frutas (Galetti, Vueltas y Pizo 2000). En mi área de investigación, tuvo lugar un acontecimiento de predación probablemente por un *Saguinus nigricollis.*

7. Identificar y poner a prueba las técnicas de gestión para reducir los impactos negativos (por ejemplo: en λ, la producción de raíces e inflorescencias) de la cosecha de raíces en las poblaciones remanentes.



Drawing by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Caqueta. In the center Bartoleme Castro weaving a creel (rigoru) (Huitoto).

Samenvatting

Drawing by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Caqueta.

Samenvatting

De ecologie van hemi-epifieten is zeer slecht bekend. De algemene levensgeschiedenis van primaire hemi-epifieten is vrij goed beschreven, maar de meeste ecologische studies hebben de secundaire hemi-epifieten tot nu toe genegeerd (Williams-Linera & Lawton 1995). Opvallend is het gebrek aan informatie over de vitale ratio en demografie van hemi-epifieten. Dergelijke informatie is essentieel om echt inzicht te krijgen in de ecologie, het beheer en het behoud van deze groep planten die een belangrijk onderdeel van het tropische kronendak vormt. In dit proefschrift heb ik getracht een aantal van deze lacunes in de kennis over de ecologie van hemi-epifieten in te vullen. Ik heb daarom drie sympatrische secundaire hemi-epifitische soorten in de Colombiaanse Amazone bestudeerd: *Heteropsis flexuosa* (Kunth) GS Bunting, *H. macrophylla* AC Sm. en *H. oblongifolia* Kunth. Ik heb voor het eerst geëvalueerd hoe zaailingen van deze soorten een gastheer vinden (hoofdstuk 2) en of deze gastheren geschikt zijn (dwz hoog genoeg) of niet. Daarna heb ik de patronen van overleving, groei, achteruitgang, vegetatieve en seksuele reproductie voor deze soorten beschreven en toegelicht, en het effect van de mate van geschiktheid van de gastheer op deze vitale ratio (hoofdstuk 3). Vervolgens analyseerde ik het relatieve belang van geschikte gastheren (die voldoende hoog zijn om *Heteropsis* te laten reproduceren) en niet-geschikte gastheren (die te laag zijn) voor de demografie van mijn studiesoorten. Tot slot heb ik, op basis van deze data, de leeftijd geschat waarop *Heteropsis*-soorten reproductief worden en wanneer hun luchtwortels kunnen worden geoogst om voor de productie van traditioneel vlechtwerk te worden gebruikt (hoofdstuk 4).

DE LEVENSCYCLUS VAN EEN SECUNDAIRE HEMI-EPIFIET (*HETEROPSIS*)

De zoektocht naar een gastheer - De levenscyclus van een secundaire hemi-epifiet kent twee contrasterende fases. De eerste vindt na kieming plaats en eindigt wanneer de zaailing een gastheer beklimt. Secundaire hemi-epifieten hebben niet de capaciteit om zichzelf rechtop te houden, en daarom hebben ze een geschikte structuur nodig om tegenop te klimmen (Putz & Holbrook, 1991). Dit vereist een effectieve zoekstrategie, idealiter één die direct resulteert in een geschikte boom waarin de klimmer zijn gehele levensduur kan blijven (Putz 1984).

Zoekstrategie - Tijdens het bestuderen van het gastheer-zoekgedrag bij *Heteropsis* vond ik dat het zoeken van de stelen of scheuten vaak onregelmatig was. Zij groeiden in willekeurige richtingen en veranderden zonder aanwijsbare reden (zoals bijvoorbeeld veranderende lichtomstandigheden of fysieke obstructie) van richting. Vrijwel geen enkele zaailing groeide in een rechte lijn. Soms vond ik groepjes van zaailingen, afkomstig uit de zaden van dezelfde vrucht, groeiend in totaal verschillende richtingen (fig. 1). Hoewel dit slechts veldwaarnemingen betreffen en er onvoldoende metingen zijn om met behulp van statistische tests te bepalen of de groeirichting van zaailingen willekeurig is, suggeren deze waarnemingen wel dat het zoeken van een gastheer een willekeurig proces is. Mijn

veldwaarnemingen van de groei van *Heteropsis*-zaailingen contrasteren met die van Strong en Ray (1975) van Monstera gigantea. Wanneer de groei van de drie soorten *Heteropsis*-zaailingen bepaald zou worden door skototropisme, zou het grootste deel van de zaailingen van dezelfde vrucht in dezelfde richting groeien, in plaats in verschillende richtingen. Verder zou het te verwachten zijn dat *Heteropsis*-zaailingen de grootste gastheren beklimmen en niet de kleinste. Het merendeel van de *Heteropsis*-zaailingen klom echter op zeer kleine en dus ongeschikte gastheren (hoofdstuk 2). Zelfs wanneer *Heteropsis*-zaailingen dichtbij hun moederplant ontkiemen, zullen de meeste van hen een ongeschikte gastheer uitkiezen. Zaailingen van Monstera, daarentegen, groeiden terug naar de gastheer van hun moeder (Ray 1976).

Ik vond een sterkere en formelere bevestiging van dit willekeurig zoekgedrag door de diameterverdeling te vergelijken tussen de gastheren van *Heteropsis*-zaailingen die net waren begonnen te klimmen en de gastheren van grotere exemplaren. Dat wijst erop dat het zoekgedrag willekeurig is. Bij *Heteropsis* juvenielen en volwassenen is dat anders: zij bevinden zich voornamelijk op grotere bomen, palmen en lianen. Verder is het percentage zaailingen dat aanwezig is op gastheren met een diameter van 10-19 cm groter dan het percentage jongeren en volwassenen in deze categorie. Deze resultaten waren consistent voor de drie soorten en suggereren een willekeurige zoekstrategie (Hoofdstuk 2). Zodra *Heteropsis* zaailingen een ongeschikte gastheer hebben beklommen, veranderen ze van gastheer door middel van vegetatieve reproductie.

De Weg Naar De Kroon

De tweede fase van de *Heteropsis* levenscyclus begint wanneer een gastheer gevonden is en de plant opstijgt door zich vast te hechten met adventieve wortels (Wilder 1992, Romero 1994; Figuur 2A). Eenmaal vastzittend aan de stam, produceert de plant een tweede type wortels. Deze absorberende wortels nemen water en voedingsstoffen op uit de bodem (fig. 2A). Zodra de absorberende wortels functioneel zijn, sterft het onderste deel van de stengel af en verliest de plant de verbinding met de bosbodem en de zaadresten (Fig. 2). Vervolgens produceert de plant plagiotropische (horizontale) takken) en nog meer absorberende wortels. De onderste delen van de stengel en de laagste wortels verouderen dan (Putz & Holbrook 1986 Plowden et al. 2003) tot de plant het onderste deel van de boomlaag (*H. oblongifolia*), of de boomkronen (*H. flexuosa* en *H. macrophylla*) bereikt.

Problemen om de kroon te bereiken? De verkeerde gastheer! - Waarschijnlijk als gevolg van de willekeurige zoekstrategie en de lage dichtheid van geschikte gastheren, beklimt de overgrote meerderheid (81%) van *Heteropsis*-zaailingen een veel te kleine en dus ongeschikte gastheer. Als gevolg kunnen deze individuen hun levenscyclus niet voltooien, want de voortplanting van *Heteropsis* is hoogte-afhankelijk (figuur 4 Hoofdstuk 2 en 3). Veel 'gastheren' van de onderzochte soorten waren dode planten, kruiden, of zaailingen van bomen. In feite klimmen de *Heteropsis*-zaailingen op alles wat ze op hun pad vinden, zelfs op afgevallen bladeren. Deze bevindingen zijn consistent met de resultaten van verschillende andere studies naar de kenmerken van gastheren van lianen (Putz 1984, Putz & Holbrook

1991, Nabe-Nielsen 2001, Sakai et al. 2002). Net zoals voor de meeste lianen (Putz 1984, 2012) en een klimmende varen, *Polybotrya pubens* Mart. (Jong en León 1991), zijn geschikte gastheren de beperkende factor voor de drie *Heteropsis*-soorten, dus de kans om een geschikte gastheer te vinden is klein (Hoofdstuk 2).

Eenmaal op de verkeerde gastheer; wat nu? Aangezien de overgrote meerderheid van de *Heteropsis*-zaailingen een ongeschikte gastheer beklimt, moeten ze een nieuwe gastheer zoeken. *Heteropsis*-planten kunnen van gastheer wisselen, als zij scheuten produceren door middel van vegetatieve vermeerdering (Figuur 5 B; hoofdstuk 2). Deze zweepachtige scheuten worden als een mechanisme voor het overwinnen van randvoorwaarden in de exploitatie van zijn habitat geïnterpreteerd (Andrade en Mayo 2000). Elk jaar produceerden tussen de 0,6 en 2,4 procent van de *Heteropsis*-individuen scheuten (ramets) die op zoek gingen naar nieuwe gastheer. De meeste van hen beklommen echter opnieuw een ongeschikte gastheer (Hoofdstuk 2). Het aandeel van ortets (genets) op een geschikte gastheer nam na de rametproductie wel toe, omdat in 35 tot 46 % van de gevallen ten minste een van de ramets een geschikte gastheer beklom. Dit betekent dat deze langlevende planten waarschijnlijk een groot aantal ramets moeten produceren om er zeker van te zijn dat tenminste één van hen een geschikte gastheer vindt, die het genetische individu kans geeft om te reproduceren. Dit fenomeen toont aan, dat het zoeken van een gastheerboom niet bij de zaailingcategorie stopt. Het is een zich herhalende, willekeurige zoekmethode door klonale vermeerdering, totdat de plant in een geschikte gastheer klimt en zijn gewenste hoogte in de (sub-) kroon (*H. flexuosa* en *H. macrophylla*) of lagere delen van de boomlaag (*H. oblongifolia*) bereikt.

Het Bereiken Van De Kroon

De vitale ratio van Heteropsis soorten - In dit hoofdstuk worden basisinzichten in de vitale ratio's (overleving, groei, vegetatieve vermeerdering en geslachtelijke voortplanting) van drie *Heteropsis*-soorten verschaft. Voor zover mij bekend is dit de eerste studie die dergelijke inzichten verschaft in de ecologie van hemi-epifieten.

Overleven - Zodra de de drie *Heteropsis*-soorten een gastheer hebben beklommen, neemt hun overlevingskans enorm toe (94 tot 85%, tabel 1), een fenomeen dat ook bij lianen is gevonden (Nabe-Nielsen 2004, Gerwing 2004). Net als andere secundaire hemi-epifieten groeien *Heteropsis*-soorten tegen de boomstam aangedrukt (figuur 2), zodat schade en mortaliteit door vallend afval wordt beperkt (Ray 1976).

Groei - Alle drie de *Heteropsis*-soorten groeiden zeer langzaam (ca. 2-8 cm hoogtegroei per jaar). Een aanzienlijk aantal individuen (tot 62%) groeit geheel niet of krimpt zelf over een periode van twee jaar (Hoofdstuk 3, Tabel 1). Deze bevindingen contrasteren sterk met de groeipercentages van rotans en lianen (Bogh 1996, Binh 2009, Nabe-Nielsen 2000, Putz 1984, 1990b, Schnitzer 2005). De langzame groei van secundaire hemi-epifieten kan mogelijk verklaard worden door de beperkte hoeveelheid voedingsstoffen en water,

die door de absorberende wortels kan worden opgenomen, maar dit blijft speculatief.

De hoeveelheid licht en het aantal wortels bleken een positieve invloed op de groeisnelheid van één van de bestudeerde soorten, *Heteropsis macrophylla*, te hebben. Vergelijkbare relaties voor groei en licht zijn voor de schaduwtolerante lianen, zoals Machaerium cuspidatum Kuhlm. & Hoehne en Connarus turczaninowii Triana (Nabe-Nielsen 2002, Aide en Zimmerman 1990), gevonden en voor zes rotanssoorten (Binh 2009, Bong 1996). Hoewel de hoogtegroei van *Heteropsis* zeker door licht wordt beperkt, kunnen tekorten aan water en voedingsstoffen een aanvullende rol spelen, gezien het effect van het aantal absorberende wortels op de groeisnelheid. Nieuwe studies tonen aan dat als volwassen *Heteropsis*-planten hoger op een gastheer klimmen, zowel het aantal als de dikte van de absorberende wortels toeneemt. Daardoor verbetert de hydraulische efficiëntie, dwz de hoeveelheid water die een bepaalde structuur (wortel, stengel, bladsteel) per eenheid van tijd en drukgradiënt kan passeren (Martínez-Vilalta and Piñol 2003, Gil-Pelegrín et al. 2005, Burgess et al. 2006). Met andere woorden, als de wortels in diameter toenemen, kunnen ze meer water vervoeren en dus een grotere hoeveelheid biomassa ondersteunen (Turriago *pers. comm.*).

Geen significante verschillen werden gevonden tussen de groeisnelheid van de drie soorten hemi-epifieten op de twee typen gastheren. In experimenten groeien lianen twee tot zeven keer sneller op geschikte gastheren (Putz 1984). Dus op de korte termijn heeft de geschiktheid van de gastheer geen invloed op de overleving en groei van de drie *Heteropsis*-soorten.

Vruchtbaarheid - Net als veel andere soorten, moeten *Heteropsis* een drempelwaarde bereiken voordat de reproductie kan beginnen (Gross 1981, Klinkhamer et al. 1987, Ohlson 1988, Primack & Hall 1990, Mendez & Obeso 1993.). De (sub-)kronendaksoorten: *H. flexuosa* en *H. macrophylla* worden reproductief en produceren bloeiwijzen op ≥ 10 m terwijl *H. oblongifolia* dit al doet op ≥ 1,5 m (hoofdstuk 2). Voor de kronendaksoorten stijgt de reproductiekans met het aantal plagiotropische takken en de hoogte. Dus, planten met dezelfde hoogte maar met meer takken produceren meer bloeiwijzen, omdat ze die aan die zijtakken produceren. Het aantal bloeiwijzen per plant was niet significant gerelateerd met hoogte voor twee van de drie soorten.

EENMAAL IN DE KROON ZIJN DE PROBLEMEN NIET VOORBIJ

Epifieten en hemi-epipifieten groeien op een zeer dynamisch substraat. Dat substraat kan in hoogte toenemen als de gastheer groeit of plotseling vernietigd worden wanneer de gastheer valt (Zotz 1998). Als de gastheer eenmaal is gevallen, overleven epifieten slechts korte tijd op de bosbodem (Matelson et al. 1993). Daarentegen kunnen *Heteropsis*-individuen wel een val van of met de gastheer overleven: tot 78% van de gevallen individuen overleefden dit gedurende mijn veldwaarnemingen. Het is niet bekend hoeveel jaar een *Heteropsis*-plant op de grond kan leven, maar enkele waargenomen individuen hadden

enkele cm diep in de strooisellaag voortdurend ramets geproduceerd, hetgeen betekent dat sommige planten jarenlang op de bosbodem kunnen overleven.

Gevallen *Heteropsis*-planten gedragen zich net als rotans (Putz 1990a) en andere lianen (90% overleving; Putz 1984). Na de val produceerden de drie *Heteropsis*-soorten vaak uitlopers, vooral in *H. oblongifolia* (46%). Hoewel gevallen epifyten niet meteen afsterven, is hun kans om ooit succesvolle nakomelingen te produceren vrijwel nihil (Hietz et al. 2002). Lianen spruiten uitbunding na een val in natuurlijke bossen en bossen met selectieve houtkap (Putz 1984, Appanah en Putz 1984). In dit opzicht gedragen de onderzochte *Heteropsis*-soorten zich meer als lianen. Dus hun levensduur wordt niet beperkt door die van hun gastheer. Individuen (genets) die de mogelijkheid hebben om te overleven na een val en nieuwe takken vormen die opnieuw een gastheer beklimmen, kunnen de dood van hun vorige gastheer dus overleven. De conclusie is dat *Heteropsis*-soorten een hoge veerkracht tegen vallende gastheren lijken te hebben. Samen met een hoge jaarlijkse overleving en een hoge uitloperproductie na een val suggereert dit dat genets van deze soorten erg oud kunnen zijn. Dit blijkt inderdaad het geval, want leeftijdsramingen op basis van matrixmodellen tonen aan dat *Heteropsis*-ramets de levensduur van 37 tot 121 jaar hebben, en dat suggereert dat dit voor genets aanzienlijk hoger zal zijn.

DEMOGRAFIE VAN DRIE *HETEROPSIS*-SOORTEN

In de vorige paragraaf heb ik laten zien dat het grootste deel van de vitale ratio's tussen mijn studiesoorten of gastheertypes niet verschilde. Echter, veel zaailingen klimmen op ongeschikte gastheren en wanneer deze planten in staat zijn om geschikte gastheren te bereiken door klonale vermenigvuldiging, is het mogelijk dat deze levenscyclus via ongeschikte gastheren sterk bijdraagt tot aan de populatiegroei-ratio (**λ**). Daarom evalueer ik in deze paragraaf de demografische gevolgen van gastheergeschiktheid op basis van drie verschillende analyses: elasticiteit (De Kroon et al., 1986; 2000; Caswell 2001), loop analyse (Güneralp 2007) en de source and sink dynamiek (Pulliam 1988; Hanski 1999). Dit is een onderwerp dat tot nu toe niet bij klimplanten is onderzocht.

De betekenis van gastheer-geschiktheid - Om de rol van de typen gastheer (geschikt en ongeschikt) op **λ** evalueren, voerde ik elasticiteit- en loop analyses uit. Volgens deze analyses zijn planten op geschikte gastheren bijzonder relevant voor **λ**. Dus het kleine percentage zaailingen dat een geschikte gastheer beklimt (19 - 28%) en overleeft tot ze de reproductieve toestand bereiken, draagt meer bij aan **λ** dan het grote aandeel zaailingen dat op ongeschikte gastheren klimmen. De drie *Heteropsis*-populaties groeien nog steeds, ondanks de willekeurige strategie waarmee ze een gastheer zoeken, het hoge percentage zaailingen dat op de grond sterft en de zeer lage dichtheid van geschikte gastheren wat uiteindelijk resulteert op zeer lage hoeveelheden jonge planten op dit type gastheer (hoofdstuk 2 en 3). De sleutel tot het voortbestaan van de populaties is waarschijnlijk de lange reproductieve levensduur van deze soorten.

Source en Sink dynamiek - Een gemeenschappelijk kenmerk van alle source-sink-modellen is dat de verschillen tussen habitats extreem zijn. In de habitat met hoge kwaliteit (de source), hebben individuen een gemiddelde fitness van meer dan 1 en deze populatie heeft gemiddeld een $\boldsymbol{\lambda} \geq 1$. De habitat van mindere kwaliteit (de sink) is zo slecht dat individuen gemiddeld een fitness van minder dan 1 hebben en, als immigratie ontbreekt, neemt de populatie af tot aan uitsterven (Diffendorfe 1998, Pulliam 1988; Hanski 1999). Bij een demografisch evenwicht (of over langere periodes), voorspellen source-sink-modellen dat de source een netto-exporteur van individuen is, terwijl de sink een netto-importeur is. Voor aanpassing van de theorie van de source-sink dynamiek naar secundaire hemi-epifieten kunnen individuen op geschikte en ongeschikte gastheren als afzonderlijke subpopulaties worden gezien. Individuen op geschikte gastheren dienen als source-populatie omdat zij kunnen reproduceren, terwijl die op ongeschikte gastheren de sink-populatie vormen, omdat zij zullen “uitsterven” bij het ontbreken van reproductie vanuit de source-populatie op geschikte gastheren. Dus, individuen die zich van een ongeschikte naar een geschikte gastheer verplaatsen verschuiven van de sink- naar de source-populatie. Ik vond aanwijzingen voor een sterke source-sink dynamiek voor de drie *Heteropsis*-soorten, want zaailingen (72-81%) en ramets (64-74%) klommen hoofdzakelijk op ongeschikte gastheren (hoofdstuk 2) en de ongunstige subpopulatie (sink) had een $\boldsymbol{\lambda} <1$ als de influx in deze subpopulaties werd geblokkeerd (hoofdstuk 4). Het hoge percentage zaailingen en ramets op ongeschikte gastheren is waarschijnlijk debet aan de grote moeilijkheid voor beide om een geschikte gastheer te vinden, wegens de willekeurige zoekstrategie en de zeer lage dichtheid van geschikte bomen (Hoofdstuk 2). Bij *Heteropsis* genereert de zoekmethode de source-sink dynamiek. De resultaten benadrukken nogmaals dat $\boldsymbol{\lambda}$ van de drie *Heteropsis*-populaties sterk afhankelijk is van de beperkte rekrutering van zaailingen op geschikte gastheren. Dit wordt bevestigd door de resultaten van de elasticiteit- en loop analyses, waaruit blijkt dat de bijdrage van de subpopulaties op geschikte gastheren veruit de grootste was voor alle drie de soorten.

Populatiegroei ratio – Mijn resultaten laten voor alle drie soorten $\boldsymbol{\lambda}$’s van 1 of hoger zien, en de populaties blijven dus stabiel of groeien bij die waarden: *H. oblongifolia*= 1.0446 (1.0025- 1.1230); *H. flexuosa* = 1.0379 (1.0000- 1.2069); *H. macrophylla* = 1.0101 (1.0000-1.1002). Vaak blijken langlevende soorten $\boldsymbol{\lambda}$-waarden van dichtbij 1 te hebben (e.g. Nabe-Nielsen 2004; Zotz 2005).

Het belang van vitale ratio’s voor populatiegroei – Ik analyseerde het relatieve belang van de vitale ratio’s voor $\boldsymbol{\lambda}$ met behulp van elasticiteitsanalyse. Deze methode wordt alom gebruikt om de relatieve bijdragen van bijvoorbeeld overleving en groei, etc., in populaties aan $\boldsymbol{\lambda}$ te meten (Franco and Silvertown 2004). Bij de drie *Heteropsis*-soorten was overleving op een geschikte gastheer de belangrijkste vitale ratio, terwijl de grootte van sexuele voortplanting en groei veel minder belangrijk bleken. Zulke resultaten zijn vaak voor houtige soorten in bossen gevonden (Caswell 2001; Silvertown et al. 1993; Silvertown & Franco 1993; Pino, Picó & Roa 2007). Mijn drie soorten reproduceerden zowel sexueel als vegetatief, waarbij sexuele reproductie veel minder belangrijk bleek dan vegetatieve. De populatiedynamica van veel soorten lijkt sterk van vegetatieve reproductie af te hangen

(Eriksson 1992; Silvertown et al. 1993; Mandujano et al. 2007; Clark-Tapia et al. 2005). Nochtans bleek reproductie bij deze drie *Heteropsis*-soorten onbelangrijk in vergelijking met het belang van overleving. Perturbatie-analyse waarbij clonale reproductie volledig werd stopgezet (K1, K2 and K3) bevestigde het geringe belang van vegetatieve reproductie voor $\boldsymbol{\lambda}$. De populatiegroei van deze soorten hing niet van K2 (de kans dat een individu een ramet produceert die naar de bosbodem afdaalt en vervolgens een gastheer beklimt en opsplitst) en K3 (de kans dat een gevallen plant een scheut produceert die uiteindelijk een gastheer van welk type dan ook beklimt en opsplitst) af. Dus de productie van ramets om een nieuwe gastheer te zoeken is in feite niet van belang voor de groei van de populatie en dat suggereert dat het aantal individuen op ongeschikte gastheren als 'onbetekend' kan worden beschouwd want ze dragen vrijwel niet aan de groei van de populatie bij. Mijn onderzoek is het eerste dat de bijdrage van vegetatieve reproductie aan de populatiegroei van secundaire hemi-epifyten evalueert.

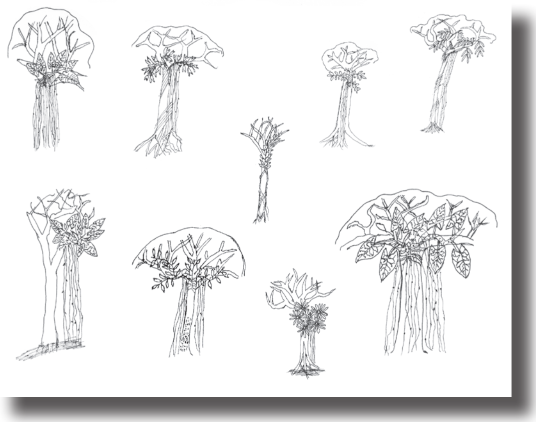
Hoe Lang Duurt Het Om Een Oogstrijpe Plant Te Worden?

Secundaire hemi-epifyten maken sterke, buigzame luchtwortels, die sinds mensenheugenis door de inheemse bevolking worden geoogst om manden, vis- en andere fuiken, bezems en bindmateriaal voor de huizenbouw van te maken (Whitehead & Godoy 1991, Bennett 1992, Paz y Miño et al. 1995, van Andel 2000, Balcázar & van Andel 2005; Fig 5). Sinds jaren worden *Heteropsis*-soorten in het gehele Amazone-gebied intensief commercieel geexploiteerd om er meubels en andere gebruiksvoorwerpen van te maken (Balcázar-Vargas and van Andel 2005, Rodrigues-Ferreira and Bentes-Gama 2005, Wallace and Ferreira 2000). *Heteropsis flexuosa* wordt veruit het meest geexploiteerd (Hoffman 1997; van Andel 2000a; Wallace & Ferreira 2000; Balcázar-Vargas & van Andel 2005), maar *H. macrophylla*, H. linearis A.C. Sm, H. longispathacea Engl., en H. spruceana Schott worden ook geoogst (Balée 1994; Paz y Miño et al. 1995; Troy & Harte 1998, Baluarte & del Castillo Torres 2001, Plowden et al. 2003, Balcázar-Vargas & van Andel 2005). Volgens de IUCN (IUCN 2012.1; http://www.iucnredlist.org) worden deze soorten op het ogenblik niet met uitsterven bedreigd. Toch worden de soorten schaars rond the dorpen waar ze geoogst worden (Balcázar-Vargas and van Andel 2005, Plowden et al. 2003).

De luchtwortels van *H. flexuosa* en *macrophylla* kunnen worden geoogst als deze hemi-epifyten een bovenste hoogte van 10 m op een gastheer hebben bereikt (Balcázar-Vargas & van Andel 2005). Mijn schatting is, dat de leeftijd waarop deze soorten zich voor het eerst voortplanten (τ) 58 jaar is, net als voor *H. flexuosa* in Guyana (Hoffman 1997) gerapporteerd wordt. *Heteropsis*-soorten bereiken hoge leeftijden (gemiddeld *H. oblongifolia*= 121, *H. flexuosa*= 37 en *H. macrophylla*= 71 jaar) en planten zich lang voort (de leeftijd waarop ze reproductief worden is: *H. oblongifolia*= 71 ±SD 86 *H. flexuosa*= 52 ±SD 91 en *H. macrophylla*= 16 ±SD 24 jaar). Omdat ze zo langzaam groeien en het zo lang duurt tot ze oogstbaar worden zijn er weinig mogelijkheden om ze te verbouwen en zo het intensieve oogsten van wilde populaties van *H. flexuosa* en *macrophylla* te vermijden. Mijn studie laat echter wel duidelijk zien dat de planten bij het oogsten niet gedood moeten worden door bijvoorbeeld alle adventiefwortels te oogsten of hele planten naar beneden te trekken.

From top to bottom and left to right: Inflorescence of *H. flexuosa*, seedling of *H. macrophylla*, adult plant of *H. tenuispadix*, Inflorescence of *H. macrophylla*, Ramet of *H. tenuispadix* climbing up a host, Chutty making marks on the host with yellow permanent paint, Inflorescence *H. tenuispadix*.

Appendix



Drawing by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Caqueta. Useful hemiepiphyte species.

APPENDIX 1. List of *Heteropsis* species found in the Biological station El Zafire. All botanical collections were deposited at the Herbario Nacional Colombiano (COL) under Maria Paula Balcazar's collector name (MPB).

Species		Collection
Heteropsis	*duckeana* M.L. Soares	MPB 1603
	ecuadorensis Sodiro	MPB 1516, 1610
	flexuosa (H.B.K.) G.S. Bunting	MPB 1513, 1615
	linearis A.C. Smith	Without collection
	macrophylla A.C. Sm	MPB 1510, 1614
	oblongifolia Kunth	MPB 1617
	reticulada Croat & M.L. Soares	MPB 1611, 1618
	rigidifolia Engl	MPB 1517
	steyermarkii G.S. Bunting	MPB 1508
	tenuispadix G.S. Bunting	MPB 1511, 1612

APPENDIX 2: Transition matrix of *Heteropsis oblongifolia.*

Matrix				Not on Host	On Host														
				Fallen individuals	Non-suitable Host					Suitable Host									
				F	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	>5,00
Not on Host	Fallen individuals	F		0,7239	0,0639	0,0645	0,0651	0,0655	0,0660	0,0090	0,0091	0,0091	0,0092	0,0093	0,0093	0,0094	0,0094	0,0095	0,0095
On Hosts	Non-suitable Hosts	1	0,01-0,25	0,1227	0,8317	0,0468	0,0196	0,0000	0,0000	0,0000	0,0000	0,0000	0,0032	0,0032	0,0963	0,1592	0,3062	0,5723	1,3006
		2	0,26-0,5	0,0289	0,0719	0,8411	0,1152	0,0303	0,0000	0,0000	0,0000	0,0000	0,0000	0,0042	0,0170	0,0281	0,0540	0,1010	0,2295
		3	0,51-0,75	0,0144	0,0000	0,0432	0,7841	0,0742	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,0345	0,7825	0,0746	0,0000	0,0000	0,0000	0,0000	0,0006	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0000	0,0393	0,8495	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Hosts	1	0,01-0,25	0,0960	0,0000	0,0029	0,0000	0,0000	0,0000	0,8389	0,0104	0,0000	0,0023	0,0000	0,0435	0,0465	0,0894	0,1671	0,3797
		2	0,26-0,5	0,0747	0,0000	0,0000	0,0000	0,0000	0,0147	0,1112	0,8485	0,0464	0,0120	0,0117	0,0050	0,0082	0,0158	0,0295	0,0670
		3	0,51-0,75	0,0427	0,0000	0,0000	0,0000	0,0083	0,0000	0,0000	0,0766	0,8338	0,0451	0,0154	0,0000	0,0000	0,0000	0,0000	0,0454
		4	0,76-1,0	0,0107	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0205	0,0540	0,8177	0,0709	0,0188	0,0191	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0033	0,0000	0,0088	0,0000	0,0065	0,0330	0,0621	0,7644	0,0923	0,0346	0,0249	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0484	0,0718	0,7938	0,1505	0,0249	0,0000	0,0312
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0368	0,0923	0,7282	0,0277	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0126	0,0000	0,0657	0,7830	0,0895	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1275	0,6170	0,0896
		10	>5,00	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2830	0,9461
				1,1139	0,9675	0,9985	1,0218	1,0001	1,0137	0,9591	0,9716	0,9763	1,0002	1,0011	1,1682	1,2496	1,4628	1,8689	3,0987

APPENDIX 3: Equations to calculate transitions of *Heteropsis oblongifolia*

Matrix				Not on Host	On Host														
				Fallen individuals	Non-suitable Host					Suitable Host									
				F	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	>5,00
Not on Host	Fallen individuals	F		P_F	FII_{NS1}	FII_{NS2}	FII_{NS3}	FII_{NS4}	FII_{NS5}	FII_{S1}	FII_{S2}	FII_{S3}	FII_{S4}	FII_{S5}	FII_{S6}	FII_{S7}	FII_{S8}	FII_{S9}	FII_{S10}
On Hosts	Non-suitable Hosts	1	0,01-0,25	$V3_{F-NS1}$	$P_{NS11}+V1_{NS11}+V2_{NS11}$	$R_{NS21}+V1_{NS21}+V2_{NS21}$	$V2_{NS31}$						$V2_{S-NS41}$	$V2_{S-NS51}$	F_{NS61}	F_{NS71}	F_{NS81}	F_{NS91}	F_{NS101}
		2	0,26-0,5	$V3_{F-NS2}$	G_{NS12}	$P_{NS22}+V1_{NS22}+V2_{NS22}$	$R_{NS32}+V1_{NS32}+V2_{NS32}$	$R_{NS42}+V1_{NS42}$						$V2_{S-NS52}$	F_{NS62}	F_{NS72}	F_{NS82}	F_{NS92}	F_{NS102}
		3	0,51-0,75	$V3_{F-NS3}$		G_{NS23}	P_{NS32}	$R_{NS43}+V1_{NS43}$											
		4	0,76-1,0				G_{NS34}	P_{NS43}	R_{NS54}					$V2S_{-NS54}$					
		5	1,01-1,5					G_{NS45}	$P_{NS55}+V1_{NS55}$										
	Suitable Hosts	1	0,01-0,25	$V3_{F-S1}$		$V2_{NS-S21}$				$P_{S11}+V_{S11}$	$R_{S21}+V1_{S21}$		$V2_{S41}$		$F_{S61}+V1_{S61}$	F_{S71}	F_{S81}	F_{S91}	F_{S101}
		2	0,26-0,5	$V3_{F-S2}$					$V2_{NS-S52}$	G_{S12}	$P_{S22}+V1_{S22}+V2_{S22}$	$R_{S31}+V1_{S31}$	$V1_{S42}+V2_{S42}$	R_{S52}	F_{S62}	F_{S72}	F_{S82}	F_{S92}	F_{S102}
		3	0,51-0,75	$V3_{F-S3}$				$V2_{NS-S43}$			$G_{S23}+V2_{S23}$	P_{S33}	$R_{S43}+V1_{S43}$	$R_{S53}+V2_{S53}$					$V1_{S103}$
		4	0,76-1,0	$V3_{F-S4}$							G_{S24}	$G_{S34}+V2_{S34}$	P_{S44}	R_{S54}	$V1_{S64}+V2_{S64}$	R_{S74}			
		5	1,01-1,5				$V2_{NS-S35}$		$V2_{NS-S55}$		G_{S25}	$G_{S34}+V2_{S35}$	G_{S45}	$P_{S55}+V1_{S55}$	R_{S65}	R_{S75}	R_{S85}		
		6	1,51-2,0										G_{S46}	G_{S56}	P_{S66}	R_{S76}	R_{S86}		$V1_{S106}$
		7	2,01-3,0											G_{S57}	G_{S67}	$P_{S77}+V1_{S77}$	R_{S87}		
		8	3,01-4,0											G_{S58}		G_{S78}	P_{S88}	R_{S98}	
		9	4,01-5,0														G_{S89}	P_{S99}	R_{S109}
		10	>5,00															G_{S910}	$P_{S1010}+V1_{S1010}$

APPENDIX 4: Elasticity matrix of *Heteropsis oblongifolia.*

Elasticity				Not on Host	On Host														
				Fallen individuals	Non-suitable Host					Suitable Host									
				F	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	>5,00
Not on Host	Fallen individuals	F		0,0298	0,0065	0,0039	0,0008	0,0001	0,0000	0,0004	0,0005	0,0003	0,0002	0,0001	0,0001	0,0001	0,0000	0,0000	0,0001
On Hosts	Non-suitable Hosts	1	0,01-0,25	0,0025	0,0419	0,0014	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0007	0,0005	0,0005	0,0007	0,0043
		2	0,26-0,5	0,0007	0,0043	0,0301	0,0009	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0001	0,0001	0,0001	0,0009
		3	0,51-0,75	0,0004	0,0000	0,0018	0,0070	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,0003	0,0010	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0000	0,0001	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Hosts	1	0,01-0,25	0,0025	0,0000	0,0001	0,0000	0,0000	0,0000	0,0225	0,0004	0,0000	0,0000	0,0000	0,0004	0,0002	0,0002	0,0002	0,0016
		2	0,26-0,5	0,0033	0,0000	0,0000	0,0000	0,0000	0,0000	0,0051	0,0494	0,0018	0,0003	0,0002	0,0001	0,0001	0,0001	0,0001	0,0005
		3	0,51-0,75	0,0027	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0064	0,0454	0,0015	0,0004	0,0000	0,0000	0,0000	0,0000	0,0005
		4	0,76-1,0	0,0011	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0028	0,0048	0,0450	0,0028	0,0006	0,0003	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0002	0,0000	0,0000	0,0000	0,0014	0,0046	0,0053	0,0479	0,0049	0,0008	0,0003	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0051	0,0055	0,0516	0,0044	0,0004	0,0000	0,0010
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0044	0,0094	0,0332	0,0006	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0040	0,0000	0,0080	0,0486	0,0042	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0141	0,0512	0,0214
		10	>5,00	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0302	0,2901

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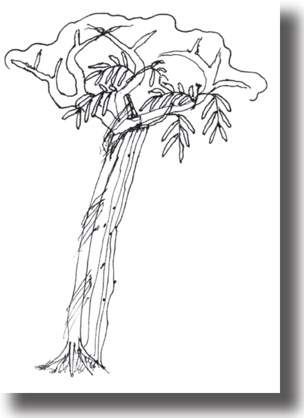

Drawing by Abel Rodriguez, Nonuya indigenous from the Peña Roja community, Middle River Caqueta. *Bejuco plancheto.*

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Ever, Chuty y yo

Curriculum Vitae

María Paula Balcázar Vargas was born on September 22, 1971 in Bogotá Colombia. In 1998, she obtained her bachelor degree in Biology at the Pontificia Universidad Javeriana in Bogotá, for her graduation thesis, she worked from 1996 to 1998 in the project Ecosystem analysis of the Serrania de Las Quinchas Puerto Boyacá, (Boyacá) at the Universidad Nacional de Colombia (Instituto de Ciencias Naturales) and the IDEAM. She was awarded with a WWF scholarship to financially support her thesis: Structure and composition of the vegetation in the Serrania de Las Quinchas, in the Magdalena Valley, Colombia. During this time she was as well curator of several families at the National Herbarium of Colombian (COL) and was fieldwork and teacher assistant of Systematic Botany courses at Universidad Nacional de Colombia. In 1997 she was research assistant in the expedition to the Hill of Miraflores, Gigante (Huila), with the same institute.

Once she graduated in May 1998 she got a job with Tropenbos-Colombia, to work in the project: Alternatives for sustainable management of non-timber products through the cultivation and harvesting of the forest canopy; case of hemiepiphyte Yaré (*Heteropsis* spp.) in indigenous communities in the middle Caquetá river (Amazonia Colombiana): a pilot study. After that in 1999 she worked in the project Development and establishment of mosses on the palm *Oenocarpus bataua* financially supported by Tropenbos-Colombia. In the same year she worked by the Etnollano Foundation at the project: Assessment of the hemiepiphytes populations used for manufacturing handicrafts by the indigenous communities Piapoco and Piaroa of the Amanavén river, Vichada, Colombia. In 2000 she was awarded with a NUFFIC scholarship to study at the Universiteit van Amsterdam for a couple of months. The next year, 2001 she worked once more by Tropenbos-Colombia in the project: Species of hemiepiphytes employed in artefacts of the material culture, by Tikuna. From 2002 to 2003 she studied English and Dutch at the Universiteit van Amsterdam (UvA).

In 2003 she started her master studies in Plant Biology at the Universiteit van Utrecht, two theses were carried out for her MSc degree, one at the Utrecht Herbarium: *Unonopsis, Bocageopsis* and *Onychopetalum* (Annonaceae). How many genera are really there? Supervised by Dr. Paul Maas & Dr. Lars Chatrou. The second study was carried out with the

Ecology and Biodiversity group: Demography of *Attalea butyracea* in the Bolivian Amazon supervised by Dr. Pieter Zuidema. She graduated from the UU in 2005. The same year she prepared a proposal for Mozaïek programme (NWO) that was awarded in 2006. In September of the same year she started the PhD; under her project she supervised many students. At the end of her PhD she got a unique opportunity to work in the project Biodiversity Virtual e-Laboratory (BioVeL) as a post-doc in the Universiteit van Amsterdam where she actually works. BioVeL is a virtual e-laboratory that supports research on biodiversity issues using large amounts of data from cross-disciplinary sources. BioVeL offers the possibility to use computerised "workflows" (series of data analysis steps) to process data, be that from one's own research and/or from existing sources. She is in charge to generate workflows to analyse matrix populations and integral projection models.

APPENDIX 2: Transition matrix of *Heteropsis flexuosa.*

Matrix				Not on Host	On Host																																					
				Fallen individuals	Non-suitable Host													Suitable Host																								
				F	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
					0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	9.01-9.99	10.0-11.0	11.01-12.0	12.01-13.0	13.01-14.0	14.01-15.0	15.01-16.0	16.01-17.0	17.01-18.0	18.01-19.0	19.01-20.0	>20
Not on Host	Fallen individuals	F		0,6786	0,0173	0,0177	0,0180	0,0182	0,0186	0,0190	0,0194	0,0197	0,0199	0,0200	0,0200	0,0201	0,0201	0,0173	0,0177	0,0180	0,0182	0,0186	0,0190	0,0194	0,0197	0,0199	0,0200	0,0200	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201	0,0201
On Hosts	Non-suitable Hosts	1	0.01-0.25	0,0671	0,7387	0,0350	0,0128	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,3690	0,5125	0,7026	0,9461	1,2426	1,5821	1,9458	2,3104	2,6558	2,9690	3,8035
		2	0.26-0.50	0,0671	0,1138	0,8047	0,0375	0,0073	0,0177	0,0000	0,0077	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0752	0,1044	0,1431	0,1927	0,2531	0,3223	0,3964	0,4706	0,5410	0,6048	0,7748
		3	0.51-0.75	0,0000	0,0000	0,0436	0,7535	0,0691	0,0091	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0171	0,0237	0,0325	0,0438	0,0575	0,0732	0,0901	0,1070	0,1230	0,1375	0,1761
		4	0.76-1.00	0,0224	0,0000	0,0056	0,0919	0,6621	0,0187	0,0000	0,0166	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1.01-1.50	0,0000	0,0000	0,0000	0,0000	0,1814	0,7480	0,0720	0,0304	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1.51-2.0	0,0224	0,0000	0,0000	0,0000	0,0151	0,1120	0,7209	0,0670	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2.01-3.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0168	0,1480	0,7426	0,0612	0,0971	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3.01-4.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1174	0,7673	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4.01-5.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1312	0,8040	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5.01-6.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1098	0,7529	0,1210	0,0624	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6.01-7.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1104	0,7558	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7.01-8.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0549	0,0552	0,0498	0,8602	0,0454	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8.01-9.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0552	0,0498	0,0555	0,9335	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Hosts	1	0.01-0.25	0,0124	0,0000	0,0008	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,7367	0,0330	0,0128	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0734	0,1020	0,1398	0,1882	0,2472	0,3148	0,3871	0,4596	0,5284	0,5907	0,7567
		2	0.26-0.50	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1138	0,7887	0,0303	0,0000	0,0103	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0073	0,0102	0,0140	0,0188	0,0247	0,0315	0,0387	0,0460	0,0528	0,0591	0,0757
		3	0.51-0.75	0,0124	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0596	0,7535	0,0691	0,0091	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0029	0,0041	0,0056	0,0075	0,0099	0,0126	0,0155	0,0184	0,0211	0,0236	0,0303
		4	0.76-1.00	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0056	0,0919	0,6621	0,0187	0,0000	0,0166	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1.01-1.50	0,0124	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1814	0,7480	0,0720	0,0304	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1.51-2.0	0,0124	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0151	0,1120	0,7209	0,0670	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2.01-3.0	0,0124	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0009	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0168	0,1480	0,7426	0,0612	0,0971	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3.01-4.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1174	0,7673	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4.01-5.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1312	0,8040	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5.01-6.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1098	0,7529	0,1210	0,0624	0,0000	0,0000	0,0000	0,0000	0,0000	0,0455	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6.01-7.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1104	0,7558	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7.01-8.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0549	0,0552	0,0498	0,7978	0,0454	0,0625	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8.01-9.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0552	0,0498	0,0555	0,7274	0,1339	0,1250	0,0000	0,0500	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		14	9.01-9.99	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0624	0,0838	0,5778	0,0000	0,0000	0,0000	0,0909	0,0556	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		15	10.0-11.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0768	0,2052	0,8963	0,0417	0,0000	0,0000	0,0000	0,0500	0,0000	0,0000	0,0000	0,0000	0,0000
		16	11.01-12.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0454	0,0000	0,0833	0,7591	0,1125	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		17	12.01-13.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0956	0,6560	0,1010	0,0000	0,0000	0,1111	0,0000	0,0000	0,0000	0,0714
		18	13.01-14.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0417	0,1079	0,5960	0,0833	0,0000	0,0000	0,0000	0,0000	0,0000	0,0833
		19	14.01-15.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1010	0,7715	0,0909	0,0556	0,1667	0,0000	0,0000	0,0000
		20	15.01-16.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1079	0,0000	0,0833	0,7721	0,0000	0,0000	0,0000	0,0000	0,0000
		21	16.01-17.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0455	0,0000	0,0455	0,8326	0,0000	0,0000	0,1250	0,0000
		22	17.01-18.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0417	0,0714	0,1250	0,8132	0,0833	0,0000	0,0000
		23	18.01-19.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0417	0,0455	0,0000	0,0000	0,0000	0,0625	0,0833	0,7715	0,0000	0,0000
		24	19.01-20.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1250	0,6882	0,0833
		25	>20	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1667	0,9084
				0,9194	0,8698	0,9073	0,9136	0,9532	0,9409	0,9597	1,0010	0,9794	1,0866	0,9937	0,9966	0,9981	0,9990	0,8678	0,9045	0,9065	0,9459	0,9334	0,9597	0,9933	0,9794	1,0857	0,9937	0,9966	0,9981	0,9990	0,9994	1,6695	1,7567	2,1375	2,3971	2,8905	3,3864	4,0803	4,4952	4,9220	5,3845	6,7836

APPENDIX 2: Transition matrix of *Heteropsis macrophylla*

Matrix				Not on Host	On Host																																							
				Fallen individuals	Non-suitable Host										Suitable Host																													
				F	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1	1,01-1,25	1,26-1,5	1,51-2	2,01-2,5	2,51-3	3,01-4	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	5,01-6,0	6,01-7,0	7,01-8,0	8,01-9,0	9,01-9,99	10,0-11,0	11,01-12,0	12,01-13,0	13,01-14,0	14,01-15,0	15,01-16,0	16,01-17,0	17,01-18,0	18,01-19,0	19,01-20,0	20,01-21,0	21,01-22,0	22,01-23,0	23,01-24,0	24,01-25,0	>25
Not on Host	Fallen individuals	F		0,7857	0,0198	0,0205	0,0209	0,0212	0,0215	0,0217	0,0218	0,0219	0,0219	0,0219	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209	0,0209
On Host	Non-suitable Host	1	0,01-0,25	0,0422	0,7761	0,0433	0,0264	0,0156	0,0000	0,0165	0,0161	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2862	0,3065	0,4664	0,7157	1,0773	1,4413	1,7160	3,0088	4,2468	4,8809	4,8811	5,2622	5,9083	6,4944	6,7100	7,1760
		2	0,26-0,5	0,0141	0,1135	0,7918	0,0594	0,0324	0,0000	0,0160	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0311	0,0333	0,0507	0,0778	0,1171	0,1567	0,1865	0,3270	0,4616	0,5305	0,5306	0,5720	0,6422	0,7059	0,7294	0,7800
		3	0,51-0,75	0,0281	0,0000	0,1051	0,6928	0,0910	0,0123	0,0165	0,0151	0,0238	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,1719	0,6274	0,0492	0,0160	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0089	0,2245	0,8024	0,0504	0,0318	0,0250	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0984	0,7511	0,0484	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1696	0,8098	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1164	0,8190	0,0333	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1338	0,8507	0,0333	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5,01-6,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1252	0,9447	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Host	1	0,01-0,25	0,0181	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,8159	0,0408	0,0229	0,0154	0,0000	0,0159	0,0154	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0187	0,0200	0,0304	0,0467	0,0703	0,0940	0,1119	0,1962	0,2770	0,3183	0,3183	0,3432	0,3853	0,4235	0,4376	0,4680
		2	0,26-0,5	0,0000	0,0000	0,0000	0,0000	0,0000	0,0022	0,0000	0,0000	0,0000	0,0000	0,0000	0,1198	0,8101	0,0595	0,0319	0,0000	0,0154	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0109	0,0117	0,0177	0,0272	0,0410	0,0548	0,0653	0,1145	0,1616	0,1857	0,1857	0,2002	0,2248	0,2471	0,2553	0,2730
		3	0,51-0,75	0,0120	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1075	0,6934	0,0897	0,0120	0,0159	0,0145	0,0228	0,0000	0,0000	0,0000	0,0598	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1721	0,6186	0,0478	0,0154	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0089	0,2213	0,7803	0,0486	0,0304	0,0239	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0957	0,7237	0,0464	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1634	0,7763	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1116	0,7838	0,0319	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0683	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1280	0,6866	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5,01-6,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2471	0,6197	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6,01-7,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,3160	0,5531	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7,01-8,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,3348	0,6795	0,0683	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8,01-9,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0478	0,2563	0,5394	0,0000	0,0000	0,3588	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		14	9,01-9,99	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,3280	0,3891	0,0000	0,0000	0,0000	0,0000	0,0531	0,0000	0,0000	0,0000	0,0000	0,0000	0,0683	0,0000	0,0000	0,0000	0,0000	0,0000
		15	10,0-11,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,4783	0,4711	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		16	11,01-12,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0683	0,3280	0,4574	0,0797	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		17	12,01-13,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1367	0,1196	0,6980	0,0000	0,0000	0,0000	0,0957	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		18	13,01-14,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1580	0,6112	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		19	14,01-15,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1965	0,5855	0,1594	0,0598	0,0000	0,0531	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		20	15,01-16,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2733	0,6168	0,0000	0,1196	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		21	16,01-17,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1196	0,0000	0,0000	0,1367	0,1594	0,5052	0,1196	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		22	17,01-18,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2153	0,4574	0,1367	0,0478	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		23	18,01-19,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1281	0,0000	0,0000	0,0598	0,2392	0,5514	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		24	19,01-20,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0598	0,6282	0,0797	0,0000	0,0000	0,0000	0,0683	0,0000
		25	20,01-21,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,1281	0,2323	0,5599	0,0000	0,0000	0,0478	0,1367	0,0000
		26	21,01-22,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0957	0,2278	0,4375	0,0598	0,0598	0,0000	0,0000
		27	22,01-23,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,2192	0,3179	0,1555	0,2477	0,0000
		28	23,01-24,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0598	0,4983	0,7564	0,0683	0,0399
		29	24,01-25,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0598	0,0000	0,0000	0,1594	0,0598	0,0598	0,3037	0,0319
		30	>25	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0598	0,0000	0,0000	0,3758	0,8959
				0,9002	0,9094	0,9607	0,9803	1,0121	0,9860	1,0580	1,0594	1,0234	1,0312	0,9999	0,9567	0,9793	0,9777	0,9980	0,9567	1,0195	1,0156	0,9795	0,9866	0,9567	0,9567	1,0165	0,9567	0,9567	1,3035	1,4477	1,5219	1,8241	2,3753	2,7035	3,1047	4,6032	6,1568	6,9405	6,8723	7,3342	8,1173	8,9711	9,3537	9,6856

APPENDIX 3: Equations to calculate transitions of *Heteropsis flexuosa*

Matrix				Not on Host	On Host																																					
				Fallen individuals	Non-suitable Host													Suitable Host																								
				F	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
					0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	9.01-9.99	10.0-11.0	11.01-12.0	12.01-13.0	13.01-14.0	14.01-15.0	15.01-16.0	16.01-17.0	17.01-18.0	18.01-19.0	19.01-20.0	>20
Not on Host	Fallen individuals	F		P_F	FII_{NS1}	FII_{NS2}	FII_{NS3}	FII_{NS4}	FII_{NS5}	FII_{NS6}	FII_{NS7}	FII_{NS8}	FII_{NS9}	FII_{NS10}	FII_{NS11}	FII_{NS12}	FII_{NS13}	FII_{S1}	FII_{S2}	FII_{S3}	FII_{S4}	FII_{S5}	FII_{S6}	FII_{S7}	FII_{S8}	FII_{S9}	FII_{S10}	FII_{S11}	FII_{S12}	FII_{S13}	FII_{S14}	FII_{S15}	FII_{S16}	FII_{S17}	FII_{S18}	FII_{S19}	FII_{S20}	FII_{S21}	FII_{S22}	FII_{S23}	FII_{S24}	FII_{S25}
On Hosts	Non-suitable Hosts	1	0.01-0.25	$V3_{F-NS1}$	$P_{NS11}+V1_{NS11}+V2_{NS11}$	$R_{NS21}+V1_{NS21}+V2_{NS21}$	$V1_{NS31}$																									F_{NS151}	F_{NS161}	F_{NS171}	F_{NS181}	F_{NS191}	F_{NS201}	F_{NS211}	F_{NS221}	F_{NS231}	F_{NS241}	F_{NS251}
		2	0.26-0.50	$V3_{F-NS2}$	G_{NS12}	$P_{NS22}+V1_{NS22}$	$R_{NS32}+V2_{NS32}$	$V2_{NS42}$	$R_{NS52}+V2_{NS52}$		$V2_{NS72}$																					F_{NS152}	F_{NS162}	F_{NS172}	F_{NS182}	F_{NS192}	F_{NS202}	F_{NS212}	F_{NS222}	F_{NS232}	F_{NS242}	F_{NS252}
		3	0.51-0.75			G_{NS23}	P_{NS33}	$R_{NS43}+V1_{NS43}$	$V1_{NS53}$																							F_{NS153}	F_{NS163}	F_{NS173}	F_{NS183}	F_{NS193}	F_{NS203}	F_{NS213}	F_{NS223}	F_{NS233}	F_{NS243}	F_{NS253}
		4	0.76-1.00	$V3_{F-NS4}$		G_{NS24}	G_{NS34}	P_{NS44}	R_{NS54}		$V1_{NS74}$																															
		5	1.01-1.50					G_{NS45}	P_{NS55}	$R_{NS65}+V1_{NS65}$	$R_{NS75}+V1_{NS75}$																															
		6	1.51-2.0	$V3_{F-NS6}$				G_{NS46}	G_{NS56}	P_{NS66}	R_{NS76}																															
		7	2.01-3.0						G_{NS57}	G_{NS67}	P_{NS77}	R_{NS87}	$V1_{NS97}$																													
		8	3.01-4.0								G_{NS78}	P_{NS88}																														
		9	4.01-5.0									G_{NS89}	P_{NS99}																													
		10	5.01-6.0										G_{NS910}	P_{NS1010}	R_{NS1110}	R_{NS1210}																										
		11	6.01-7.0											G_{NS1011}	P_{NS1111}																											
		12	7.01-8.0										G_{NS912}	G_{NS1012}	G_{NS1112}	P_{NS1212}	R_{NS1312}																									
		13	8.01-9.0											G_{NS1013}	G_{NS1113}	G_{NS1213}	P_{NS1313}																									
	Suitable Hosts	1	0.01-0.25	$V3_{F-S1}$		$V2_{NS2-S1}$												$P_{S11}+V1_{S11}$	$R_{S21}+V1_{S21}$	$V1_{S31}$												F_{S151}	F_{S161}	F_{S171}	F_{S181}	F_{S191}	F_{S201}	F_{S211}	F_{S221}	F_{S231}	F_{S241}	F_{S251}
		2	0.26-0.50															G_{S12}	$P_{S22}+V1_{S22}$	R_{S32}		R_{S52}										F_{S152}	F_{S162}	F_{S172}	F_{S182}	F_{S192}	F_{S202}	F_{S212}	F_{S222}	F_{S232}	F_{S242}	F_{S252}
		3	0.51-0.75	$V3_{F-S3}$															G_{S23}	P_{S33}	$R_{S43}+V_{S43}$	$V1_{S53}$										F_{S153}	F_{S163}	F_{S173}	F_{S183}	F_{S193}	F_{S203}	F_{S213}	F_{S223}	F_{S233}	F_{S243}	F_{S253}
		4	0.76-1.00																G_{S24}	G_{S34}	P_{S44}	R_{S54}		$V1_{S74}$																		
		5	1.01-1.50	$V3_{F-S5}$																	G_{S45}	P_{S55}	$R_{S65}+V_{S65}$	$R_{S75}+V_{S75}$																		
		6	1.51-2.0	$V3_{F-S6}$																	G_{S46}	G_{S56}	P_{S66}	R_{S76}																		
		7	2.01-3.0	$V3_{F-S7}$									$V2_{NS9-S7}$									G_{S57}	G_{S67}	P_{S77}	R_{S87}	$V1_{S97}$																
		8	3.01-4.0																					G_{S78}	P_{S88}																	
		9	4.01-5.0																						G_{S89}	P_{S99}																
		10	5.01-6.0																							G_{S910}	P_{S1010}	R_{S1110}	R_{S1210}						R_{S1810}							
		11	6.01-7.0																								G_{S1011}	P_{S1111}														
		12	7.01-8.0																							G_{S912}	G_{S1012}	G_{S1112}	P_{S1212}	R_{S1312}	R_{S1412}											
		13	8.01-9.0																								G_{S1013}	G_{S1113}	G_{S1213}	P_{S1313}	R_{S1413}	$V1_{S1513}$		$V1_{S1713}$								
		14	9.01-9.99																										G_{S1214}	G_{S1314}	P_{S1414}				R_{S1814}	$V1_{S1914}$						
		15	10.0-11.0																											G_{S1315}	G_{S1415}	P_{S1515}	R_{S1615}				$V1_{S32015}$					
		16	11.01-12.0																											G_{S1316}		G_{S1516}	P_{S1616}	$R_{S1716}+V_{S1716}$								
		17	12.01-13.0																														G_{S1617}	P_{S1717}	R_{S1817}			$V1_{S2117}$				R_{S2517}
		18	13.01-14.0																														G_{S1618}	G_{S1718}	P_{S1818}	R_{S1918}						$V1_{S2518}$
		19	14.01-15.0																																G_{S1819}	P_{S1919}	R_{S2019}	$V1_{S2119}$	$R_{S2219}+V_{S2219}$			
		20	15.01-16.0																															G_{S1720}		G_{S1920}	P_{S2020}					
		21	16.01-17.0																																G_{S1821}		G_{S2021}	P_{S2121}			R_{S2421}	
		22	17.01-18.0																																	G_{S1922}	G_{S2022}	G_{S2122}	P_{S2222}	R_{S2322}		
		23	18.01-19.0																														G_{S1623}	G_{S1723}				G_{S2123}	G_{S2223}	P_{S2323}		
		24	19.01-20.0																																					G_{S2324}	P_{S2424}	$V1_{S2524}$
		25	>20																																						G_{S2425}	P_{S2525}

Appendix 3: Equations to calculate transitions of *Heteropsis macrophylla*

Matrix				Not on Host	On Host																																							
				Fallen individuals	Non-suitable Host										Suitable Host																													
				F	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1	1,01-1,25	1,26-1,5	1,51-2	2,01-2,5	2,51-3	3,01-4	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	5,01-6,0	6,01-7,0	7,01-8,0	8,01-9,0	9,01-9,99	10,0-11,0	11,01-12,0	12,01-13,0	13,01-14,0	14,01-15,0	15,01-16,0	16,01-17,0	17,01-18,0	18,01-19,0	19,01-20,0	20,01-21,0	21,01-22,0	22,01-23,0	23,01-24,0	24,01-25,0	>25
Not on Host	Fallen individuals	F		P_F	FII_{NS1}	FII_{NS2}	FII_{NS3}	FII_{NS4}	FII_{NS5}	FII_{NS6}	FII_{NS7}	FII_{NS8}	FII_{NS9}	FII_{NS10}	FII_{S1}	FII_{S2}	FII_{S3}	FII_{S4}	FII_{S5}	FII_{S6}	FII_{S7}	FII_{S8}	FII_{S9}	FII_{S10}	FII_{S11}	FII_{S12}	FII_{S13}	FII_{S14}	FII_{S15}	FII_{S16}	FII_{S17}	FII_{S18}	FII_{S19}	FII_{S20}	FII_{S21}	FII_{S22}	FII_{S23}	FII_{S24}	FII_{S25}	FII_{S26}	FII_{S27}	FII_{S28}	FII_{S29}	FII_{S30}
On Host	Non-suitable Host	1	0,01-0,25	$V3_{F-NS1}$	$P_{NS11}+ V2_{NS11}$	$R_{NS21}+ V2_{NS21}$	$R_{NS31}+V1_{NS31}+ V2_{NS31}$	R_{NS41}		$V1_{NS61}$	$V1_{NS71}$																				F_{NS171}	F_{NS181}	F_{NS191}	F_{NS201}	F_{NS211}	F_{NS221}	F_{NS231}	F_{NS241}	F_{NS251}	F_{NS261}	F_{NS271}	F_{NS281}	F_{NS291}	F_{NS301}
		2	0,26-0,5	$V3_{F-NS2}$	G_{NS12}	$P_{NS22} + V1_{NS22}$	R_{NS32}	$R_{NS42} + V1_{NS42}$		R_{NS62}																					F_{NS172}	F_{NS182}	F_{NS192}	F_{NS202}	F_{NS212}	F_{NS222}	F_{NS232}	F_{NS242}	F_{NS252}	F_{NS262}	F_{NS272}	F_{NS282}	F_{NS292}	F_{NS302}
		3	0,51-0,75	$V3_{F-NS3}$		G_{NS23}	$P_{NS33}+ V1_{NS33}$	$R_{NS43} + V1_{NS43}$	R_{NS53}	$V1_{NS63}$	$V1_{NS73}$	$V1_{NS83}$																																
		4	0,76-1,0				G_{NS34}	P_{NS44}	R_{NS54}	R_{NS64}																																		
		5	1,01-1,5				G_{NS35}	G_{NS45}	P_{NS55}	$R_{NS65} + V1_{NS65}$	$R_{NS75} + V1_{NS75}$	R_{NS85}																																
		6	1,51-2,0						G_{NS56}	P_{NS66}	$R_{NS76} + V1_{NS76}$																																	
		7	2,01-3,0							G_{NS67}	P_{NS77}																																	
		8	3,01-4,0								G_{NS178}	P_{NS88}	R_{NS98}																															
		9	4,01-5,0									G_{NS89}	$P_{NS99} + V1_{NS99}$	R_{NS109}																														
		10	5,01-6,0										G_{NS910}	P_{NS1010}																														
	Suitable Host	1	0,01-0,25	$V3_{F-S1}$											P_{S11}	R_{S21}	$R_{S31} +V1_{S31}$	R_{S41}		$V1_{S61}$	$V1_{S61}$										F_{S171}	F_{S181}	F_{S191}	F_{S201}	F_{S211}	F_{S221}	F_{S231}	F_{S241}	F_{S251}	F_{S261}	F_{S271}	F_{S281}	F_{S291}	F_{S301}
		2	0,26-0,5						$V2_{NS5-S2}$						G_{S12}	$P_{S22} + V1_{S22}$	R_{S32}	$R_{S42} +V1_{S42}$		R_{S62}											F_{S172}	F_{S182}	F_{S192}	F_{S202}	F_{S212}	F_{S222}	F_{S232}	F_{S242}	F_{S252}	F_{S262}	F_{S272}	F_{S282}	F_{S292}	F_{S302}
		3	0,51-0,75	$V3_{F-S1}$												G_{S23}	$P_{S33} + V1_{S33}$	$R_{S43} +V1_{S43}$	R_{S53}	$V1_{S61}$	$V1_{S61}$	$V1_{S61}$				$V1_{S61}$																		
		4	0,76-1,0														G_{S34}	P_{S44}	R_{S54}	R_{S64}																								
		5	1,01-1,5														G_{S35}	G_{S45}	P_{S55}	$R_{S65} +V1_{S65}$	$R_{S75} +V1_{S75}$	R_{S85}																						
		6	1,51-2,0																G_{S56}	P_{S66}	$R_{S76} +V1_{S76}$																							
		7	2,01-3,0																	G_{S67}	P_{S77}																							
		8	3,01-4,0																		G_{S78}	P_{S88}	R_{S98}											$V1_{S61}$									
		9	4,01-5,0																			G_{S89}	$P_{S99} + V1_{S99}$																					
		10	5,01-6,0																				G_{S910}	P_{S1010}																				
		11	6,01-7,0																					G_{S1011}	P_{S1111}																			
		12	7,01-8,0																						G_{S1112}	P_{S1212}	R_{S1312}																	
		13	8,01-9,0																						G_{S1113}	G_{S1213}	P_{S1313}			$R_{S1613} +V1_{S1613}$														
		14	9,01-9,99																								G_{S1314}	P_{S1414}					$V1_{S61}$						R_{S2514}					
		15	10,0-11,0																									G_{S1415}	P_{S1515}															
		16	11,01-12,0																									G_{S1416}	G_{S1516}	P_{S1616}	R_{S1716}													
		17	12,01-13,0																										G_{S1517}	G_{S1617}	P_{S1717}				R_{S2117}									
		18	13,01-14,0																												G_{S1718}	P_{S1818}												
		19	14,01-15,0																													G_{S1819}	$P_{S1919} + V1_{S31919}$	R_{S2019}	R_{S2119}		$V1_{S61}$							
		20	15,01-16,0																														G_{S1920}	P_{S2020}		R_{S2220}								
		21	16,01-17,0																											G_{S1621}			G_{S1921}	G_{S2021}	P_{S2121}	R_{S2221}								
		22	17,01-18,0																																G_{S2122}	P_{S2222}	R_{S2322}	R_{S2422}						
		23	18,01-19,0																													G_{S1823}			G_{S2123}	G_{S2223}	P_{S2323}							
		24	19,01-20,0																																		G_{S2324}	P_{S2424}	R_{S2524}				R_{S2924}	
		25	20,01-21,0																																		G_{S2325}	$G_{S2425} + V1_{S2425}$	P_{S2525}			$V1_{S61}$	$R_{S2925} +V1_{S2925}$	
		26	21,01-22,0																																			G_{S2426}	G_{S2526}	P_{S2626}	R_{S2726}	R_{S2826}		
		27	22,01-23,0																																					G_{S2627}	P_{S2727}	$R_{S2827} +V1_{S2827}$	$R_{S2927} +V1_{S2927}$	
		28	23,01-24,0																																					G_{S2628}	G_{S2728}	P_{S2828}	$V1_{S61}$	R_{S3028}
		29	24,01-25,0																																		G_{S2329}			G_{S2629}	G_{S2729}	G_{S2829}	P_{S2929}	$V1_{S61}$
		30	>25																																					G_{S2630}			G_{S2930}	P_{S3030}

APPENDIX 4: Elasticity matrices of *Heteropsis flexuosa.*

Elasticity				Not on Host	On Host																																					
				Fallen individuals	Non-suitable Host													Suitable Host																								
				F	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
					0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	0.01-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.50	1.51-2.0	2.01-3.0	3.01-4.0	4.01-5.0	5.01-6.0	6.01-7.0	7.01-8.0	8.01-9.0	9.01-9.99	10.0-11.0	11.01-12.0	12.01-13.0	13.01-14.0	14.01-15.0	15.01-16.0	16.01-17.0	17.01-18.0	18.01-19.0	19.01-20.0	>20
Not on Host	Fallen individuals	F		0,0018	0,0003	0,0003	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
On Hosts	Non-suitable Hosts	1	0.01-0.25	0,0000	0,0014	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0001	0,0001	0,0000	0,0001
		2	0.26-0.50	0,0000	0,0003	0,0015	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		3	0.51-0.75	0,0000	0,0000	0,0001	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0.76-1.00	0,0000	0,0000	0,0000	0,0001	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1.01-1.50	0,0000	0,0000	0,0000	0,0000	0,0000	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1.51-2.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2.01-3.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3.01-4.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4.01-5.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5.01-6.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6.01-7.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7.01-8.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8.01-9.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Hosts	1	0.01-0.25	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0005	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		2	0.26-0.50	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0002	0,0006	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		3	0.51-0.75	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0005	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0.76-1.00	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0002	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1.01-1.50	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0002	0,0012	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1.51-2.0	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0003	0,0018	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2.01-3.0	0,0005	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0007	0,0038	0,0001	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3.01-4.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0013	0,0036	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4.01-5.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0011	0,0039	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5.01-6.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0006	0,0068	0,0004	0,0009	0,0000	0,0000	0,0000	0,0000	0,0000	0,0006	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6.01-7.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0010	0,0027	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7.01-8.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0004	0,0006	0,0002	0,0146	0,0020	0,0011	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8.01-9.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0010	0,0003	0,0015	0,0491	0,0037	0,0128	0,0000	0,0016	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		14	9.01-9.99	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0019	0,0063	0,0179	0,0000	0,0000	0,0000	0,0027	0,0032	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		15	10.0-11.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0086	0,0094	0,1526	0,0037	0,0000	0,0000	0,0000	0,0024	0,0000	0,0000	0,0000	0,0000	0,0000
		16	11.01-12.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0040	0,0000	0,0112	0,0539	0,0046	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		17	12.01-13.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0086	0,0340	0,0045	0,0000	0,0000	0,0042	0,0000	0,0000	0,0000	0,0026
		18	13.01-14.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0030	0,0045	0,0212	0,0058	0,0000	0,0000	0,0000	0,0000	0,0000	0,0024
		19	14.01-15.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0041	0,0616	0,0041	0,0019	0,0112	0,0000	0,0000	0,0000
		20	15.01-16.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0063	0,0000	0,0081	0,0419	0,0000	0,0000	0,0000	0,0000	0,0000
		21	16.01-17.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0037	0,0000	0,0040	0,0575	0,0000	0,0000	0,0065	0,0000
		22	17.01-18.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0041	0,0039	0,0053	0,0664	0,0051	0,0000	0,0000
		23	18.01-19.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0044	0,0028	0,0000	0,0000	0,0000	0,0027	0,0070	0,0490	0,0000	0,0000
		24	19.01-20.0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0117	0,0331	0,0052
		25	>20	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0103	0,0720

APPENDIX 4: Elasticity matrices of *Heteropsis macrophylla*

Elasticity				Not on Host	On Host																																							
				Fallen individuals	Non-suitable Host										Suitable Host																													
				F	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
					0,01-0,25	0,26-0,5	0,51-0,75	0,76-1	1,01-1,25	1,26-1,5	1,51-2	2,01-2,5	2,51-3	3,01-4	0,01-0,25	0,26-0,5	0,51-0,75	0,76-1,0	1,01-1,5	1,51-2,0	2,01-3,0	3,01-4,0	4,01-5,0	5,01-6,0	6,01-7,0	7,01-8,0	8,01-9,0	9,01-9,99	10,0-11,0	11,01-12,0	12,01-13,0	13,01-14,0	14,01-15,0	15,01-16,0	16,01-17,0	17,01-18,0	18,01-19,0	19,01-20,0	20,01-21,0	21,01-22,0	22,01-23,0	23,01-24,0	24,01-25,0	>25
Not on Host	Fallen individuals	F		0,0027	0,0002	0,0001	0,0001	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
On Host	Non-suitable Host	1	0,01-0,25	0,0000	0,0023	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0002	0,0000	0,0002
		2	0,26-0,5	0,0000	0,0005	0,0028	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		3	0,51-0,75	0,0001	0,0000	0,0005	0,0017	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,0005	0,0011	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0000	0,0005	0,0024	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0004	0,0013	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0003	0,0012	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0008	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0011	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5,01-6,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0020	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
	Suitable Host	1	0,01-0,25	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0040	0,0002	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0001
		2	0,26-0,5	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0009	0,0069	0,0003	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0001
		3	0,51-0,75	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0051	0,0003	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		4	0,76-1,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0018	0,0034	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		5	1,01-1,5	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0001	0,0017	0,0073	0,0002	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		6	1,51-2,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0018	0,0050	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		7	2,01-3,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0017	0,0057	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		8	3,01-4,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0052	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		9	4,01-5,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0015	0,0031	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		10	5,01-6,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0022	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		11	6,01-7,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0017	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		12	7,01-8,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0030	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		13	8,01-9,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0002	0,0015	0,0032	0,0000	0,0000	0,0011	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		14	9,01-9,99	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0025	0,0020	0,0000	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000	0,0000	0,0000	0,0000	0,0006	0,0000	0,0000	0,0000	0,0000	0,0000
		15	10,0-11,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0028	0,0024	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		16	11,01-12,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0004	0,0019	0,0023	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		17	12,01-13,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0009	0,0007	0,0042	0,0000	0,0000	0,0000	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		18	13,01-14,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0022	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		19	14,01-15,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0006	0,0022	0,0006	0,0003	0,0000	0,0002	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		20	15,01-16,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0009	0,0019	0,0000	0,0003	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		21	16,01-17,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0010	0,0000	0,0000	0,0006	0,0006	0,0026	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		22	17,01-18,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0014	0,0019	0,0006	0,0004	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		23	18,01-19,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0009	0,0000	0,0000	0,0006	0,0016	0,0037	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
		24	19,01-20,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0005	0,0108	0,0034	0,0000	0,0000	0,0000	0,0027	0,0000
		25	20,01-21,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0010	0,0038	0,0224	0,0000	0,0000	0,0082	0,0050	0,0000
		26	21,01-22,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0024	0,0139	0,0289	0,0060	0,0156	0,0000	0,0000
		27	22,01-23,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0169	0,0370	0,0474	0,0163	0,0000
		28	23,01-24,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0054	0,0674	0,2680	0,0052	0,0119
		29	24,01-25,0	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0008	0,0000	0,0000	0,0123	0,0070	0,0183	0,0201	0,0082
		30	>25	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0032	0,0000	0,0000	0,0173	0,1609