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Reproductive Ecology, Seedling Performance, and Population Structure of *Parkia pendula* in an Atlantic Forest Fragment in Northeastern Brazil

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The day passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has been wandering by himself in a Brazilian forest. Among the multitude of striking objects, the general luxuriance of the vegetation bears away the victory. The elegance of the grasses, the novelty of the parasitic plants, the beauty of the flowers, the glossy green of the foliage all tend to this end. A most paradoxical mixture of sound and silence pervades the shady parts of the wood. The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore; yet within the recesses of the forest a universal silence appears to reign. To a person fond of natural history, such a day as this, brings with it a deeper pleasure than he ever can hope again to experience.

Charles Darwin's first impressions of a tropical rainforest;
Atlantic Forest of Bahia, Brazil; February 29, 1832.
(Darwin C. 1839. Voyage of the Beagle; reprinted 1989 by Penguin Books, London)

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Acknowledgments

Finally, after more than four years of work I finished my thesis. This would not have been possible without the help of many people. Herewith I wish to express my deepest thanks to all who have directly or indirectly contributed to this work.

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Summary

The highly diverse Atlantic Forest stretches across 27 degrees of southern latitude along the Brazilian coastline and originally covered almost 15% of the national territory. Meanwhile, more than 92% of this biome have been destroyed and the remaining forests are extremely fragmented. This is especially true for the forests in northeastern Brazil, where the forest covers less than 5% of its original extent. The remaining forest fragments are usually surrounded by sugarcane fields. Forest fragmentation affects the survival of plant and animal species in various ways. For example, flora and fauna are exposed to larger variations of soil humidity at newly created edges than in the forest interior.

Parkia pendula is a widespread tree species of Neotropical lowland rainforests. It occurs from the Atlantic Forest of the Brazilian state of Espírito Santo towards Honduras in Central America. The striking trees of this species are typical of the Atlantic Forest of the state of Pernambuco in northeastern Brazil. Like most species of this Pantropical genus, *P. pendula* is pollinated by large, unspecialized bats.

The goal of the present study was to investigate edge effects on several phases of the life cycle of the abundant species *P. pendula*. Additionally, the pollination ecology of this species was studied in detail since little is known about the pollination of Neotropical tree species that are pollinated by large, unspecialized bats. The study was conducted in a 319 ha forest fragment on the property of a sugarcane plantation north of Recife, the capital of Pernambuco.

The mean bud development of *P. pendula* lasted for ten weeks. Approx. 90% of the inflorescence buds were aborted at the beginning of this period, while later on approx. 90% of the remaining capitulum buds were aborted. This resulted in inflorescences with a mean number of 1.6 capitula. A rapid growth of the respective organs started immediately after the abortion phases. The final inflorescence length of 118 cm was reached one week before the flowering night. These flagellate inflorescences extend far into the spacious free airspace underneath the flat *P. pendula* crowns. The trees flowered an average of three weeks during the main flowering period from the beginning of September to the end of October. Trees in the forest edge zone bore six times as many capitula as the trees in the forest interior although there were no differences in height, diameter, and crown area between the individuals of the two habitats. An additional enrichment of the forest edge zone with water and nutrients from the nearby artificial irrigation of the sugarcane fields is likely to be responsible for the higher number of capitula in the forest edge zone. A period with a nearly doubled precipitation during the early bud development phases was probably the reason for a low flowering amplitude during the second year of

observation (2004). Nearly all observed trees flowered during the first year of observation (2003), whereas only 16% of the trees in the forest edge zone and no tree in the forest interior flowered in 2004.

A mean capitulum of *P. pendula* consisted of 1,065 flowers. Three quarters of these flowers were fertile and hermaphrodite, one quarter sterile and nectar-secreting. The elongated styles of the sterile flowers are a morphological device to prevent the nectar from dropping. Self-incompatibility was proved experimentally. The floral odor was mainly composed of monoterpenes, with *trans*-ß-ocimene as the dominating compound. The significant change in floral odor during the nocturnal anthesis is interpreted as a sign of flower aging. No sulphur containing odor compounds were detected. Sulphur compounds are often found in floral odors of chiropterophilous plants and permit bats the precise, short distance localization of single flowers. Bats achieved the localization of the long, freely hanging inflorescences of *P. pendula* most probably by their visual and echolocating senses instead.

The nectar production began at dusk and reached a median volume of 7.4 ml per capitulum until its end around 03:00 h. This volume is similar to the nectar volumes of other *Parkia* species irrespective of the species-specific capitulum size or the number of nectar-secreting flowers. These volumes are interpreted as an adaptation to obtain a maximum number of visits by large bats. A total nectar production of up to 42 l was calculated per tree and flowering period. The nectar's sugar content was composed of the two monosaccharides glucose and fructose and the disaccharide sucrose with a total mean concentration of 15.9%. The ratio of mono- to disaccharides changed during the nocturnal anthesis as well as the nectar's amino acid composition. This kind of qualitative change of the nectar composition during anthesis was previously known for very few plant species only.

The large bat species *Phyllostomus discolor* (Phyllostominae) was the main pollinator of *P. pendula* with up to 466 visits per capitulum and night. These bats always approached the freely hanging capitula steeply from below, landed briefly and dropped away backwards into the free airspace afterwards again. The steep rise and the later fall always resulted in a vertical movement of the bats of 2-5 m underneath the capitula. This space-demanding trajectory is presumably the reason for the species' avoidance of less freely hanging capitula. It is assumed that this free airspace of several meters depth underneath the tree crowns is due to *P. pendula* repressing the growth of the sub-canopy trees. This assumption is supported by the recent finding of growth-repressing substances in *P. pendula*. Thus, the free airspace is a precondition for the main pollinator to reach the capitula and carry out pollination because of its space-demanding flight. Although visits by the bat species *Phyllostomus hastatus* (Phyllostominae) and *Platyrrhinus lineatus* (Stenodermatinae) occurred seldom,

they were also occasional pollinators. The bat species *Glossophaga soricina* (Glossophaginae) acted as nectar-thief at capitula of *P. pendula*. This species mainly visited the less freely hanging capitula that were avoided by *Phyllostomus discolor*. Additionally to the bat species, the mammals *Coendou prehensilis*, *Caluromys philander*, *Nasua nasua*, and *Callithrix jacchus* visited the capitula of *P. pendula* and fed either on capitulum buds or on nectar. This emphasizes the importance of *P. pendula* for the arboreal mammal fauna of the studied Atlantic Forest fragment.

The number of *P. pendula* pods decreased drastically due to abortion at the beginning of the nine weeks lasting pod development. Exudation of the sticky seedpod gum started two months after flowering. A huge number of seeds remained on the pods after pod opening because they were glued to the very sticky exudate or were still connected with the pods by their funicles. The complete leaf shedding occurred simultaneously with the fruit ripening at the end of the dry season. The begin of leaf shedding, and the dates of total defoliation and newly foliated crowns took place two to four weeks earlier in the forest interior than in the forest edge zone during the first year of observation. During the second year of observation, this shift was significant for newly foliated crowns only. Since defoliation is commonly a result of water stress, earlier leaf shedding was expected to occur in the forest edge zone due to lower soil moisture. However, this common microclimatic edge effect was compensated during the dry season in the study area by a heavy irrigation of the adjacent sugarcane fields with liquid residua from the industrial sugar production. The seed production of *P. pendula* differed significantly between the habitats as a consequence of the difference in the number of capitula. Compared with the forest interior, the seed production per standardized crown area was 12 times higher in the forest edge zone.

The fate of *P. pendula* seeds after dropping on the forest floor was experimentally investigated in the forest edge zone and in the forest interior. The time until seeds were removed from the experimental sites was significantly longer in the forest edge zone than in the forest interior (21 days *vs.* 9 days). On-site predation contributed only little to the disappearance of the seeds and was equal for all treatments. The ant species *Pachycondyla crassinoda* was observed to transport the seeds. A survey of the leaf-litter ant fauna revealed a much higher abundance of *P. crassinoda* in the forest interior. The avoidance of the forest edge zone by this ant species is presumably the reason for the lower secondary seed dispersal in the forest edge zone.

The median total number of *P. pendula* seedlings underneath the adult tree crowns was significantly higher in the forest edge zone probably due to the higher seed production. The germination rate, that is the ratio of seedlings per produced seeds, as well as the number of seedlings remote from the mother trees were

significantly higher in the forest interior compared with the forest edge zone. Additionally, the survival of the seedlings is significantly longer and the seedlings tend to have more leaves in the forest interior. The higher leaf litterfall in the forest edge zone could be the reason for the lower germination rate and survival time since a thicker leaf layer on the forest floor is known to reduce the germination rate and burying of *P. pendula* seedlings under dead leaves mostly resulted in the death of the seedlings. Saplings (individuals <2 m in height, which had already lost their first, simplified foliage leaf) were the most abundant size class of *P. pendula* in the forest edge zone and the forest interior. Their density was equal between habitats, whereas the density of juvenile trees (juvenile individuals >2 m) was higher in the forest edge zone.

It can be summarized that most studied processes of the life cycle of *P. pendula* were negatively affected by the proximity to the forest edge. The secondary seed dispersal as well as the germination rate and the seedling growth (measured by the number of leaves) were lower in the forest edge zone compared with the forest interior. Additionally, the seedling mortality was higher in the forest edge zone. Nevertheless, these effects were partly compensated by the higher seed production, which was presumably caused by an influx of nutrients from the surrounding sugarcane fields. However, older individuals seem to profit from edge effects that occurred after seedling establishment, as indicated by the higher density of juvenile trees in the forest edge zone.

Zusammenfassung

Der hochdiverse Atlantische Regenwald Brasiliens erstreckt sich über 27 Breitengrade entlang der Küste und bedeckte ursprünglich fast 15% des Landes. Mittlerweile ist dieses Biom zu über 92% zerstört und die noch existierenden Wälder sind hochgradig fragmentiert. Besonders weit fortgeschritten ist die Zerstörung dieser Wälder im Nordosten Brasiliens. Hier ist die ursprüngliche Waldbedeckung auf unter 5% gesunken. Die verbliebenen Waldfragmente sind meist von Zuckerrohrfeldern umgeben. Die Fragmentierung von Wäldern beeinträchtigt das Überleben vieler Pflanzen- und Tierarten auf unterschiedliche Weise. So sind Flora und Fauna an den neu geschaffenen Waldrändern beispielsweise größeren Schwankungen der Bodenfeuchtigkeit als im Waldesinneren ausgesetzt.

Parkia pendula ist eine weit verbreitete Baumart neotropischer Tieflandregenwälder. Das Verbreitungsgebiet erstreckt sich vom brasilianischen Bundesstaat Espírito Santo an der Atlantikküste bis nach Honduras in Mittelamerika. Die auffälligen Bäume dieser Art sind typisch für den Atlantischen Regenwald des Bundesstaates Pernambuco im Nordosten Brasiliens. Wie fast alle Arten dieser pantropischen Gattung wird auch *P. pendula* von großen, unspezialisierten Fledermäusen bestäubt.

Die vorliegende Arbeit hatte zum Ziel, die Einflüsse des Waldrandes auf verschiedene Phasen des Lebenszyklus der häufigen Art *P. pendula* zu untersuchen. Des Weiteren wurde die Bestäubungsökologie dieser Art detailliert studiert, da bisher nur wenig über die Bestäubung von neotropischen Baumarten durch große, unspezialisierte Fledermäuse bekannt ist. Die Untersuchungen wurden in einem 319 ha großen Waldfragment auf dem Gelände einer Zuckerrohrplantage nördlich der Landeshauptstadt von Pernambuco, Recife, durchgeführt.

Die Knospenentwicklung bei *P. pendula* dauerte durchschnittlich zehn Wochen. In dieser Zeitspanne wurden anfangs rund 90% der angelegten Infloreszenzknospen abgeworfen, später rund 90% der noch vorhandenen Capitulumsknospen, so dass jede Gesamtinfloreszenz im Durchschnitt noch 1,6 Capitula besaß. Unmittelbar nach den jeweiligen Abstoßungsphasen setzte das Längenwachstum der verbliebenen Organe ein. Eine Woche vor der Blühnacht war die endgültige Länge der Gesamtinfloreszenz von 118 cm erreicht. Diese flagellaten Infloreszenzen reichen weit in den ausgedehnten freien Luftraum unterhalb der flachen *P. pendula* Kronen. Die Hauptblühphase, in der jeder Baum durchschnittlich drei Wochen blühte, lag zwischen Anfang September und Ende Oktober. Bäume in der Waldrandzone produzierten fast sechsmal mehr Capitula als die Bäume im Waldesinneren, obwohl sich die Individuen zwischen den Standorten weder in

Höhe, Durchmesser noch Kronenfläche unterschieden. Ein erhöhter Eintrag von Wasser und Nährstoffen durch die Bewässerung der umgebenden Zuckerrohrfelder in die Waldrandzone scheint für die größere Anzahl an Blütenständen ausschlaggebend zu sein. Eine Periode mit der annähernd doppelten normalen Niederschlagsmenge während der frühen Knospenentwicklungsphasen war vermutlich der Grund für eine sehr geringe Blühintensität im zweiten Beobachtungsjahr. Im ersten Beobachtungsjahr blühten fast alle der beobachteten Bäume, wohingegen 2004 nur 16% der Bäume in der Waldrandzone und keiner im Waldesinneren blühte.

Ein durchschnittliches Capitulum von *P. pendula* hatte 1.065 Blüten. Drei Viertel dieser Blüten waren fertil und zwittrig, ein Viertel steril und nektarsekretierend. Der gestreckte Griffel der sterilen Blüten verhindert das Abtropfen des Nektars. Selbstinkompatibilität wurde experimentell nachgewiesen. Der Blütenduft setzte sich hauptsächlich aus Monoterpenen zusammen und wurde von *trans*-ß-Ocimen dominiert. Die signifikante Änderung der Duftzusammensetzung im Laufe der nächtlichen Anthese wird als Zeichen des Alterungsprozesses der Blüten interpretiert. Schwefelhaltige Duftkomponenten, die häufig in Blütendüften fledermausbestäubter Arten nachgewiesen werden, wurden nicht gefunden. Fledermäuse können dank solcher Schwefelduftstoffe Blumen gut kleinräumig lokalisieren. Das Auffinden der langen, weit in den freien Luftraum unterhalb der Baumkronen hineinragenden Infloreszenzen von *P. pendula* erfolgt hingegen wahrscheinlich optisch und mittels Echoortung.

Die Nektarproduktion begann in der Dämmerung, endete gegen 03:00 Uhr und erreichte ein durchschnittliches Volumen von 7,4 ml Nektar pro Capitulum. Diese Menge entspricht den Nektarvolumina anderer *Parkia*-Arten, unabhängig von der artspezifischen Größe der Capitula oder der Anzahl der nektarsekretierenden Blüten. Diese hohen Nektarvolumina werden als Anpassung interpretiert eine maximale Anzahl an Besuchen großer Fledertiere zu erzielen. Pro Baum und Blühperiode wurde eine Gesamtnektarmenge von bis zu 42 l berechnet. Der Zuckeranteil im Nektar bestand aus den zwei Monosacchariden Glukose und Fruktose sowie dem Disaccharid Saccharose mit einer durchschnittlichen Gesamtkonzentration von 15,9%. Das Verhältnis dieser Einfach- und Zweifachzucker zueinander veränderte sich im Laufe der nächtlichen Anthese ebenso wie die Aminosäurenzusammensetzung des Nektars. Derartige qualitative Änderungen des Nektars während der Anthese waren bisher nur bei sehr wenigen Pflanzenarten bekannt.

Die große Fledermausart *Phyllostomus discolor* (Phyllostominae) war mit bis zu 466 Besuchen pro Capitulum und Nacht der Hauptbestäuber von *P. pendula*. Diese Fledermaus flog die frei unter der Baumkrone hängenden Capitula immer steil von

unten an, landete kurz und ließ sich danach wieder rückwärts in den freien Luftraum fallen. Die vertikale Bewegung der Fledermäuse unter den Capitula durch den steilen Aufwärtsflug und das anschließende Fallenlassen betrug immer 2-5 m. Dieser raumgreifende Flug ist vermutlich der Grund für die Meidung von weniger frei hängenden Capitula durch *P. discolor*. Es wird angenommen, dass dieser mehrere Meter tiefe freie Luftraum unter den Baumkronen durch ein von *P. pendula* verursachtes gehemmtes Wachstum der unter den *Parkia*-Kronen wachsenden Bäume entsteht. Kürzlich bei *P. pendula* nachgewiesene wachstumshemmende Substanzen untermauern diese Vermutung. Aufgrund seines raumgreifenden Fluges ermöglicht es erst der freie Luftraum dem Hauptbestäuber, *Phyllostomus discolor*, die Capitula von *P. pendula* zu erreichen und somit zu bestäuben. Obwohl die Fledermausarten *Phyllostomus hastatus* (Phyllostominae) und *Platyrrhinus lineatus* (Stenodermatinae) nur äußerst selten die Capitula besuchten, kommen sie jedoch ebenfalls als Gelegenheitsbestäuber infrage. Die Fledermausart *Glossophaga soricina* (Glossophaginae) hingegen war lediglich Nektarräuber und besuchte hauptsächlich die von *Phyllostomus discolor* gemiedenen, schwerer zugänglichen Capitula. Neben den Fledermäusen besuchten weitere Säuger wie *Coendou prehensilis*, *Caluromys philander*, *Nasua nasua* und *Callithrix jacchus* die Blütenstände von *P. pendula* und fraßen entweder an den Capitulumsknospen oder tranken den Nektar. Dies unterstreicht die Bedeutung von *P. pendula* für die auf Bäumen lebenden Säugetiere im untersuchten Fragment des Atlantischen Regenwaldes.

Zu Beginn der neunwöchigen Fruchtentwicklung wurde die Anzahl der Hülsenfrüchte von *P. pendula* stark reduziert. Die Absonderung des klebrigen Hülsenexsudates begann zwei Monate nach dem Abblühen. Nach der Öffnung der Hülsen verblieben viele Samen in den Hülsen, da sie entweder am Exsudat festklebten oder durch ihre Funikel noch mit den Hülsen verbunden waren. Zeitgleich mit der Fruchtbildung fand auch der völlige Laubwechsel zum Ende der Trockenperiode statt. Der Beginn des Blattabwurfes, die Zeitpunkte der völligen Entlaubung und der neu belaubten Kronen waren im Waldesinneren im ersten Beobachtungsjahr zwei bis vier Wochen früher als in der Waldrandzone. Diese Verschiebung war im zweiten Jahr nur für die neu belaubten Kronen signifikant. Da Wasserstress ein häufiger Grund für Blattabwurf ist, wurde wegen der geringeren Bodenfeuchte eine frühere Entlaubung in der Waldrandzone erwartet. Dieser übliche abiotische Randeffekt wurde während der Trockenzeit jedoch durch die starke Bewässerung der angrenzenden Zuckerrohrfelder mit den flüssigen Rückständen der industriellen Zuckerproduktion ausgeglichen. Die Samenproduktion von *P. pendula* unterschied sich entsprechend der Unterschiede in der Anzahl der Capitula ebenfalls signifikant zwischen den beiden Habitaten. Im

Waldrandbereich war die Samenproduktion pro standardisierter Kronenfläche 12 mal höher als im Waldesinneren.

Der Verbleib der zu Boden gefallenen *P. pendula* Samen wurde experimentell sowohl in der Waldrandzone als auch im Waldesinneren untersucht. Die Samen in der Waldrandzone blieben signifikant länger an der Stelle auf dem Waldboden liegen, an der sie ausgebracht wurden, als die Samen im Waldesinneren (21 Tage gegenüber 9 Tagen). Der Parasitierungsgrad war überall gleich und trug nur zu einem kleinen Teil zum Verschwinden der Samen bei. Ameisen der Art *Pachycondyla crassinoda* wurden beim Transport der Samen beobachtet. Eine Untersuchung der laubstreubewohnenden Ameisengesellschaft zeigte, dass *P. crassinoda* deutlich häufiger im Waldesinneren aufzufinden war. Die Meidung der Waldrandzone durch diese große Ameisenart ist vermutlich der Grund für die geringere sekundäre Ausbreitung von *P. pendula* Samen in der Waldrandzone.

Die Gesamtzahl der *P. pendula* Keimlinge unter den Mutterbäumen war in der Waldrandzone aufgrund der höheren Samenproduktion signifikant höher als im Waldesinneren. Die Keimungsrate, also das Verhältnis der Keimlinge pro produzierten Samen, sowie die Keimlingsdichte abseits der Mutterbäume waren jedoch im Waldesinneren signifikant höher. Hier überlebten die Keimlinge auch signifikant länger und hatten tendenziell mehr Laubblätter. Der höhere Laubfall in der Waldrandzone könnte ein Grund für die geringere Keimung und die kürzere Überlebenszeit sein, da eine mächtigere Laubstreu häufig die Keimung reduziert und von Laub begrabene *P. pendula* Keimlinge meist abstarben. Schösslinge, also alle Individuen unter 2 m Höhe, die ihr Primärblatt bereits verloren hatten, waren die häufigste Größenklasse von *P. pendula* in der Waldrandzone sowie im Waldesinneren. Ihre Dichte unterschied sich nicht zwischen den Habitaten, wohingegen die der Jungbäume (noch nicht fertile Individuen >2 m) in der Waldrandzone höher war.

Zusammenfassend zeigte sich, dass die Nähe zum Waldrand auf die meisten der untersuchten Prozesse des Lebenszyklus von *P. pendula* negative Auswirkungen hat. Die sekundäre Samenausbreitung sowie die Keimung und das Keimlingswachstum (gemessen an der Anzahl der Laubblätter) waren in der Waldrandzone geringer als im Waldesinneren, wohingegen die Keimlingssterblichkeit in der Waldrandzone höher war. Diese Effekte wurden jedoch teilweise durch die höhere Samenproduktion in der Waldrandzone kompensiert, die vermutlich auf einen Nährstoffeintrag von den umgebenden Feldern zurückzuführen ist. Ältere Individuen scheinen jedoch von nach der Keimlingsetablierung auftretenden Randeffekten zu profitieren, wie die höhere Jungbaumdichte in der Waldrandzone zeigt.

1. Introduction

1.1. The Genus *Parkia*

The Pantropical mimosoid genus *Parkia* consists of 33 species and several subspecies (Hopkins 1983a, 1986a, 1994), but many more taxa are expected to exist, especially in the Amazon basin (Hopkins 1998, M.J.G. Hopkins pers. comm.), its center of diversity (Baker and Harris 1957, Hopkins 1998). Several *Parkia* species are known to co-exist in these forests (Hopkins 1984, 1986a). For example, the floristically best studied Amazonian terra-firme forest, the Reserva Florestal Ducke, a 10,000 ha reserve situated in the direct neighborhood of Manaus, harbors seven *Parkia* species (Ribeiro et al. 1999), which is the highest known α-diversity for this genus. Most *Parkia* species are canopy trees of lowland rainforests but both, savanna species (*P. platycephala* and *P. biglobosa*) and a shrub species (*P. cachimbensis*) are also known (Hopkins 1986a, Pettersson and Knudsen 2001).

The flowers of all *Parkia* species are organized in globose heads (capitula). The occurrence and arrangement of the three existing flower types (fertile, nectar-secreting, and staminodial) at these capitula are the basis of the further division of this genus into three sections (Hopkins 1986a). The species of the largest section, *Parkia*, have biglobose capitula consisting of all three flower types (Hopkins 1986a), and occur in South America as well as in Africa and Southeast Asia, whereas the other two sections, *Platyparkia* and the paraphyletic '*Spaeroparkia*' (Luckow and Hopkins 1995), occur only in South America (Hopkins 1998). '*Spaeroparkia*' species have fertile flowers only and are thought to be basal in the genus, whereas the capitula of *Platyparkia* species consist of fertile and nectar-secreting flowers (Hopkins 1998).

Probably most attention was paid to this genus because of its bat-pollination of almost certainly all species of the sections *Parkia* and *Platyparkia*. Starting in the 1920s, chiropterophily was suspected – mainly by van der Pijl and Porsch – to be a regular pollination system in the tropics (Dobat and Peikert-Holle 1985). Before that, the few casually (but partially very detailed) observations of bat visits at flowers were interpreted to be exceptions and not the rule (Dobat and Peikert-Holle 1985). Geographically, the center of the majority of the more thorough observations during the first decades of the last century was Southeast Asia, especially the Botanical Garden of Buitenzorg (today Bogor) in Java (Dobat and Peikert-Holle 1985). *Parkia speciosa* was among these trees in Buitenzorg and was found to be pollinated by pteropodid bats (Danser 1929, Docters van Leeuwen 1933, van Heurn 1929, van der Pijl 1936). Pteropodidae were also found to be the pollinators of the African species *P. biglobosa* (Baker and Harris 1957). The Neotropical species – in the absence of pteropodid bats – were supposed to be pollinated by Phyllostomidae (Baker and Harris 1957, Vogel 1954), which was verified by de Carvalho (1960, 1961) for *P.*

gigantocarpa and *P. pendula* and by Vogel (1968) for *P. discolor*. These findings of a Pantropical, relatively homogenous genus, which is pollinated by two very distantly related bat groups, one of them probably younger than the separation of South America from Africa, lead to a discussion about the evolutionary history and distribution of the genus *Parkia*, as well as of flower-visiting bats and chiropterophily in general. This discussion is known as the '*Parkia* mystery' or '*Parkia* problem' (Baker 1973, Baker and Harris 1957, Vogel 1969). More recently, after a number of publications on the pollination ecology of some African and Neotropical *Parkia* species (Grünmeier 1990, 1992, Hopkins 1983a, 1984, Pettersson et al. 2004, Pettersson and Knudsen 2001), their taxonomy and distribution (Hopkins 1983a, 1986a, 1994), as well as their seed and fruit ecology (Hopkins 1983a, Hopkins and Hopkins 1983), there are some indications by cladistic analyses for a South American origin of the genus *Parkia* and two transatlantic dispersal events of the section *Parkia* (Hopkins 1998, Luckow and Hopkins 1995). Nevertheless, an evolution from a Gondwanian-distributed common ancestor, which was pollinated by ancient non-flying mammals is still widely accepted for some taxa, including *Parkia* (von Helversen and Winter 2003).

Several *Parkia* species have local economic importance. Seeds of *P. speciosa* and *P. biglobosa* are eaten as vegetable in Southeast Asia and West Africa, respectively (Danser 1929, Hopkins 1983a, 1994). The pods of *P. platycephala* are an important forage crop for cattle in the northeastern Brazilian caatinga region (Hopkins 1986a). Some species are also used to some degree by the timber industry in South America and Southeast Asia (Angelo et al. 2004, Hopkins 1994, Martini et al. 1994).

1.1.1 *Parkia pendula*

Parkia pendula (Willd.) Benth. ex Walp. is the most widely distributed Neotropical *Parkia* species, occurring in lowland terra-firme forests from Honduras in Central America southwards to the Atlantic Forest of the Brazilian state of Espírito Santo (Hopkins 1986a). *Parkia pendula* is also a typical (de Andrade-Lima 1960, Ferraz et al. 2004, Siqueira et al. 2001) and abundant (Guedes 1998, Lins-e-Silva 1996, Siqueira et al. 2001) species of the Atlantic Forest's endemism center of Pernambuco (Cardoso da Silva and Casteleti 2003). Its density in this region is much higher than in the Amazonian forests (Peres 2000, M.J.G. Hopkins pers. comm.).

The adult trees are easily recognizable by their very distinctive flattened crown (Ribeiro et al. 1999). The mass-flowering species (Hopkins 1984) presents its red capitula on long axes underneath the crowns (Hopkins 1986a) what makes it one of the most beautiful trees of the Amazon basin (Hopkins 1986b, Ribeiro et al. 1999).

Parkia pendula is known to be pollinated by bats. Nine phyllostomid bat species were recorded from *P. pendula* until now by de Carvalho (1961), Hopkins (1984), and Rodriguez-H. and Hopkins (2000) with *Phyllostomus discolor* being probably the main pollinator (de Carvalho 1961, Hopkins 1984). The only record of pollinator quantity is by Hopkins (1984). She once saw a large flock of several hundred bats suddenly disappearing from a flowering *P. pendula* individual. Beside the bats, medium-sized non-flying mammals were observed visiting flowering capitula of *P. pendula* (Hopkins 1984).

The pods of *P. pendula* (together with that of its close congener *P. paraensis*) are unique since they secrete large quantities of a sticky amber-colored gum, into which the seeds are released after dehiscence of the pods (Hopkins 1986a, Hopkins and Hopkins 1983). This gum is a source of protein, carbohydrates, calcium, and magnesium (Anderson and de Pinto 1985, Peres 2000) for parrots and primates, which act thereby as seed dispersers (summarized in Peres 2000). The small seeds, which have a hard testa exhibiting a conspicuous horseshoe line (Peres 2000), maintain normal germination rates after several months of submersion and anoxia. Seedlings survive water logging and submersion only a few weeks (Scarano and Crawford 1992). A mechanically pre-germination damage of the testa such as scarification raised the germination rate drastically in some studies (Barbosa et al. 1984, Scarano and Crawford 1992) but had no effect on germination rate or time in another (Schulze 2003).

The seedlings are fast-growing in forest gaps with low mortality rates (Schulze 2003), making the species one of the favorite ones for forest restoration projects (Camargo et al. 2002, Knowles and Parrotta 1995, Parotta and Knowles 2001, Schulze 2003). Not only the seedling growth rates are relatively high, but also the average growth rate of the adult trees is known to be one of the highest within large Amazonian emergent trees (Chambers et al. 1998). This might be related to the relatively low wood density of *P. pendula* (Melo Nogueira et al. 2005, Schulze 2003). Despite its light wood, this species is a valuable timber species in the Amazon basin (Angelo et al. 2004, Martini et al. 2004, Schulze 2003). Beside the use as timber, lectin of *P. pendula* has some use as a histochemical marker (Beltrão et al. 2003, Lombardi et al. 1998).

1.2. The Atlantic Forest

The Brazilian Atlantic Forest (Port.: Mata Atlântica) extends from the northeastern state of Rio Grande do Norte to the southernmost state of Rio Grande do Sul, a distribution along 27 degrees of southern latitude from 3°S to 30°S (Pinto and de Brito 2003). It contains a wide range of abiotic conditions due to this very wide

expansion. This region encompasses an altitudinal gradient from sea level to elevations higher than 2,700 m in the Mantiqueira and Caparaó Mountains in the states of São Paulo, Minas Gerais, Rio de Janeiro, and Espírito Santo. The climate varies from subhumid regimes with dry seasons in the northeastern states to the highest Brazilian precipitation values of approx. 4,000 mm at the eastern slopes of the southern coastal mountains (Câmara 2003). These conditions resulted in a biodiversity mosaic, composed of numerous vegetation types (Pinto and de Brito 2003) ranging from the coastal rainforests and *Araucaria* forests to high-altitude grasslands (Câmara 2003). This broad definition of the Atlantic Forest biome was established at a workshop in 1990 and encompasses inland forests of Argentina and Paraguay as well (Câmara 2003). This biome once covered 1,363,000 km² in Brazil, or nearly 15% of the Brazilian territory (Hirota 2003).

Up to now, the Atlantic Forest has lost > 92% of its original area. The remaining 100,000 km² are highly fragmented with larger forest sites in the rugged terrain of the southern states Rio de Janeiro, São Paulo, and Santa Catarina (Hirota 2003, Morellato and Haddad 2000). Consequently, this biogeographic region (Serra do Mar) still has about 30% of its original extension (Galindo-Leal and Câmara 2003), including the largest continuous forest of the Atlantic Forest biome (Aguiar et al. 2003). The forest destruction is worst in the northeastern biogeographic region Pernambuco, which encloses all coastal Atlantic Forest north of the São Francisco River (states of Alagoas, Pernambuco, Paraiba, and Rio Grande do Norte), with only 4.82% of the original forest cover left (Cardoso da Silva and Casteleti 2003). All these percentages of forest cover include not only the few primary forest formations but also forests planted with exotic species and secondary forests in various stages of regeneration (Câmara 2003).

The destruction of the Atlantic Forest begun with the Portuguese colonization in the sixteenth century with their intensive logging of Brazilwood (*Caesalpinia echinata*). After its extraction, the northeastern forests were cleared for cultivation of the introduced sugarcane (*Saccharum officinarum*) and for firewood to fuel the sugar mills, which continues to be the economic basis of northeastern Brazil until now (Dean 1995, Frickmann Young 2003, Guedes et al. 2005). One reason for the high economic value of sugarcane is the ethanol-program of the Federal government, which was implemented in the 1970s to become more independent of petrol (Marris 2006). Beside sugarcane in the Northeast, cattle, gold, and coffee were the commodities the Atlantic Forest was logged for (Frickmann Young 2003). Together with the ongoing increase in agriculture (Galindo-Leal and Câmara 2003), human population density raised. Brazil's largest agglomerations, São Paulo, Rio de Janeiro, Belo Horizonte, Curitiba, Recife, Salvador de Bahia, all of them with more than 3 million inhabitants, are all situated within the Atlantic Forest region

(da Rocha 2005). The area of the Brazilian Atlantic Forest today is occupied by 106 million people, or more than 60% of the country's total population (Hirota 2003).

The wide expansion of the Atlantic Forest with its great variety of abiotic factors together with an evolutionary history with alternating periods of connection with other South American forests and clear separations through savanna vegetation (Cardoso da Silva and Casteleti 2003, Gottsberger and Silberbauer-Gottsberger 2006a) resulted in an unique biota with numerous endemic species (Cardoso da Silva and Casteleti 2003, Myers et al. 2000). In their extensive comparison of the earth's biodiversity hotspots, Myers et al. (2000) summarize 20,000 plant species in the Atlantic Forest, of which 8,000 (40%) are endemic to this region. Of the 1,361 vertebrate species (without fishes) 567 (41.7%) are endemic to the Brazilian Atlantic Forest (Myers et al. 2000). Both, plant and vertebrate endemics contribute to more than 2% of the total species world-wide (Myers et al. 2000). This enormous biodiversity is not distributed homogeneously within the Atlantic Forest. A biogeographic classification based on the distribution of endemic species of the well known groups of forest birds, primates, and butterflies led to an identification of five endemism centers: Brejos Nordestinos, Pernambuco, Diamantina, Bahia, and Serra do Mar (Cardoso da Silva and Casteleti 2003), which corresponds well with a phytogeographic definition (Guedes et al. 2005). The Atlantic Forest is declared to be within the top five of the world's 'hottest hotspots' (Myers et al. 2000) due to the very high biodiversity and endemism rates and the enormous habitat loss. This ranking elucidates the massive importance of this region for the world's biodiversity and its very threatened status.

The number of protected areas of Atlantic Forest has risen dramatically over the past 40 years from 50 in 1960 to 676 in 2000 (Galindo-Leal and Câmara 2003). Unfortunately, these numbers do not mean much since approx. 75% of all these conservation units are smaller in size than 100 ha and most of them lack an efficient biodiversity management, being therefore only 'paper parks' (Galindo-Leal and Câmara 2003). This is especially true for the northeastern endemism centers Pernambuco and Brejos de Altitude, predestining these regions to be given top priority for conservation actions like creation of new conservation units, restoration, and connection of the remaining fragments through corridors (Cardoso da Silva and Casteleti 2003, Galindo-Leal and Câmara 2003).

1.3. Forest Fragmentation

Starting in the 1970s, biodiversity and conservation research begun to focus on the consequences of large-scale deforestation of tropical forests. This scientific focus originated from the debate about the question of whether one large reserve could

preserve more species than several small reserves adding up to the equivalent area of the larger reserve (the so-called SLOSS or 'single large or several small' debate), based on the island biogeography theory by MacArthur and Wilson (1967) (Saunders et al. 1991). This debate led into the creation of the experimental 'Biological Dynamics of Forest Fragments Project' (BDFFP) near Manaus (Bierregaard Jr and Gascon 2001, Laurance and Bierregaard Jr 1997), which is the longest-running and largest fragmentation experiment world-wide (Debinski and Holt 2000). The original focus of this project was almost exclusively on possible area effects but it broadened as the complexity of fragmentation effects became apparent (Lovejoy et al. 1986).

Several 'fragmentation factors' (Zuidema et al. 1996) with major effects on the fragment's biota have since been identified in the BDFFP and numerous other projects world-wide. Here, the five most important fragmentation factors are summarized, following the reviews by Laurance and Vasconcelos (2004), Murcia (1995), Saunders et al. (1991), and Zuidema et al. (1996).

Area effects

Larger forest fragments generally contain a higher diversity of the original biota than smaller fragments because of four reasons. Firstly, forest fragments are samples of a larger area and may exclude just by chance patchily distributed species that were present in the original area (sample effects). Secondly, larger forest fragments support more niches for species and this generally means more species will be present. Thirdly, the probability of viable populations is higher in larger fragments due to a higher number of individuals. Fourthly, the influence of edge effects is higher in smaller fragments. Species that are sensitive to edge effects are therefore excluded from smaller fragments.

Distance effects

Non-forested vegetation between forest fragments can act as a strong barrier. The interfragment distance that acts as a dispersal barrier strongly depends on the species' mobility, behavior, and dispersal mechanism or pollination agent. Isolated populations are vulnerable to random demographic events, inbreeding, genetic drift, and are therefore prone to locally extinction with only a very reduced possibility to be reestablished by other subpopulation of the region's metapopulation.

Edge effects

Forest fragmentation unavoidably leads to the creation of artificial and abrupt edges were previously there where none. Three types of edge effects on the forest biota can be distinguished. Firstly, there are abiotic effects like changes in the microclimate resulting from the proximity to a structurally dissimilar matrix. Secondly, the

abundance and distribution of some species will change due to the abiotic changes. These direct biological effects are determined by the physiological tolerances of the species. Thirdly, the changes in species abundance and distribution may have cascading effects on other species due to species interactions like pollination or seed dispersal (indirect biological effects).

Matrix effects

The kind of the vegetation that surrounds forest fragments (matrix) has great influences on the magnitude of distance and edge effects. In general, the more closely the matrix approximates the structure of the primary forest, the lower are the distance and edge effects on the forest biota.

Synergistic effects

Most tropical fragments are located in anthropogenic landscapes and are therefore used by humans for logging, hunting, and extraction of non-timber forest products. Additionally, these fragments are also subjected to incursions of fire and other human disturbances from the outside. Such simultaneous environmental changes can interact additively or synergistically, leading to even greater impacts on the forest populations.

1.4. Hypotheses and Aims of the Study

There has been some debate during the last years whether research on single species or on the ecosystem as a whole is more promising in conservation research (aut- *vs.* synecology). Both approaches have their specific strengths but also clear limitations (summarized in Lindenmayer et al. 2007), wherefore a combination of both approaches is highly recommended for research projects, especially for research on the biological consequences of habitat fragmentation (Fischer and Lindenmayer 2007, Saunders et al. 1991). The design of the binational research project "Sustainability of remnants of Atlantic rainforest in Pernambuco and its implications for conservation and regional development" encompasses both approaches in its research on possible edge effects on the biota of Atlantic Forest fragments. The Brazilian research group concentrates on patterns (Rodal and Lins-e-Silva 2003), especially on patterns of plant species distribution in relation to forest edges (e.g., Silva 2004, Silva 2005). The German research group works mainly on the single species level within the framework of the Brazilian pattern-oriented work, focussing on processes like pollination, seed dispersal, and germination (Gottsberger 2003), which may explain some of the patterns found by the counterparts. The present study is one of the species-oriented works within this project.

The focus species of this study, *Parkia pendula*, was chosen because of two reasons. Firstly, it is one of the most common and important tree species in the forest fragment 'Piedade' (Silva 2005) and the whole endemism center of Pernambuco (Ferraz et al. 2004, Guedes 1998). Secondly, the genus *Parkia* is recommended for autecological research by Hartshorn (1990) due to the occurrence of ecologically similar species of this genus at several research sites world-wide. Therefore, the study has not only a local importance but its results may be compared with similar studies on this genus elsewhere.

The present study on *P. pendula* has two levels of research interest. The first part of this work (chapter 3) tries to elucidate the pollination ecology of *P. pendula*. The aim was to obtain data on odor and nectar production comparable to the studies on *P. biglobosa* in western Africa by Pettersson and Knudsen (2001) and on *P. bicolor* (Pettersson et al. 2004). Beside the enlargement of former knowledge on the pollination ecology of *P. pendula* by de Carvalho (1961) and Hopkins (1984), this first part also aimed to get new insights into the pollination by 'big bats' (von Helversen 1993) in the Neotropics since research so far mainly focused on pollination by glossophagine bats (von Helversen and Winter 2003).

The study's second part (chapters 4-6) aimed to answer the question, if different processes within the life cycle of *P. pendula* are affected by edge effects and if these possible differences are reflected in the species' population structure. Most attention was paid to potential differences in phenology and seed production (chapter 4), secondary seed dispersal (chapter 5), and germination and seedling establishment (chapter 6).

2. Study Site and General Study Design

2.1. Usina São José

This study was conducted on the property of the sugarcane plantation Usina São José S/A, in the periphery of the metropolitan area of Recife, the capital of the northeastern Brazilian state of Pernambuco (Figure 1). The total area of the Usina São José is about 247 km² (07°41'05"-07°54'42"S, 34°54'18"-35°05'07"W; Trinidade et al. 2007). This area contains 106 remnants of Atlantic Forest, which cover 27% (66.6 km²) of the Usina's area (Trinidade et al. 2007). The matrix that surrounds the fragments consists of monocultural sugarcane fields.

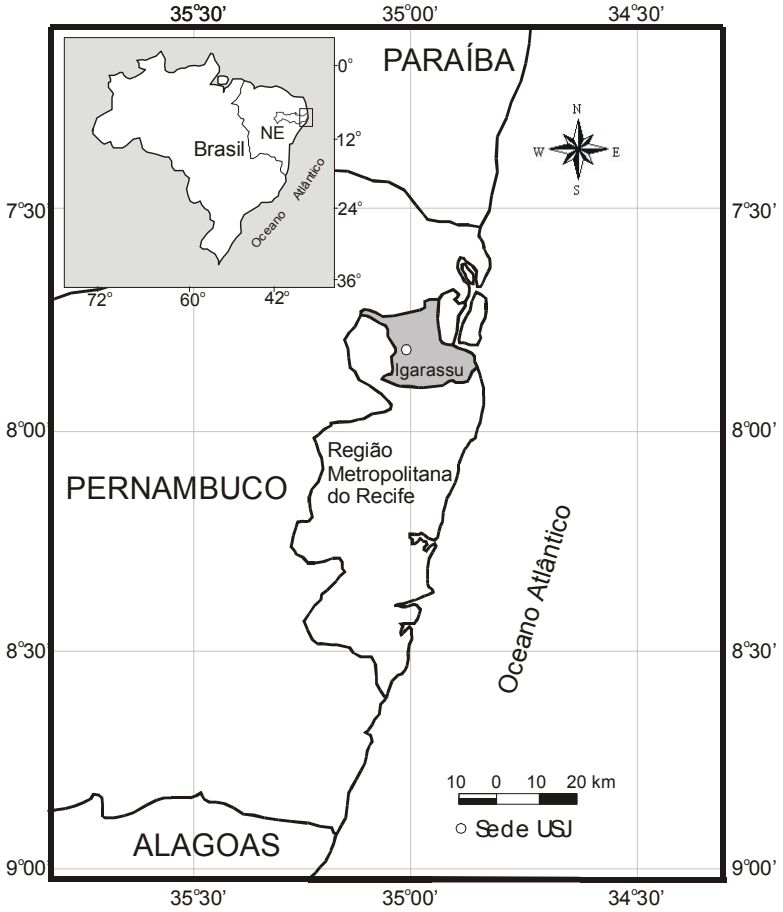

Figure 1 Location of the Usina São José S/A (USJ) (after Trinidade et al. 2007).

An analysis of a time series of areal photographs revealed that about 50% of the forest destruction on the São José area proceeded during the last 30 years (Trinidade 2005), most probably as a direct result of the ethanol-program of the Federal government in the 1970s (Marris 2006). Almost all forest fragments are separated from the plantations by small cart-tracks (Schessl et al. in press). The majority (52%) of the fragments have a size of 10 to 100 ha, but most of the total forest cover (69.3%) is located in the few fragments which are larger than 100 ha (Trinidade et al. 2007). Another characteristic of these fragments is their irregular

shape. Most of the 106 Atlantic Forest fragments (69%) are very irregularly shaped, i.e., their ratio of circumference to area is less than 0.4 (Trinidade et al. 2007).

The climate of this region is characterized by a rainy season from January to August and a dry season from September to December and is therefore noticeably seasonal. The annual air temperature is relatively constant at approx. 25°C (Figure 2).

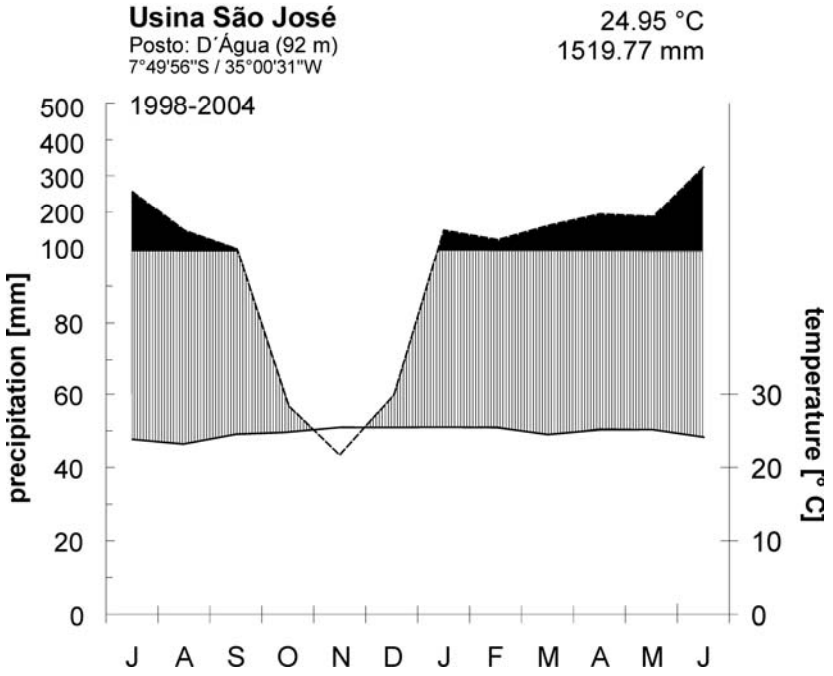

Figure 2 Climatic diagram of the pluviometric station 'D'Agua' near the forest fragment 'Piedade' with monthly mean values of temperature and precipitation (after Schessl et al. in press).

Despite this clear pattern of annual rainfall, there are strong variations in annual precipitation ranging from 770 mm in 1998 to 2,960 mm in 2004 (Schessl et al. in press). Furthermore, there exists an enormous spatial gradient in rainfall recorded by the 14 pluviometric stations that are operated by the Usina São José. Highest average annual rainfall values were measured near the coastline (2,600 mm) and lowest (1,520 mm) just 11 km inland and 90 m uphill (Schessl et al. in press).

2.2. Forest Fragment 'Piedade'

The forest fragment 'Piedade' with an area of 319 ha is one of the largest forest fragments on the property of the Usina São José and is located near the Usina's southern border (7°49'16"-7°50'54"S, 34°49'26"-35°00'35"W; Schessl et al. in press). An analysis of a time series of areal photographs revealed that the 'Piedade' fragment is relatively old since its shape and size have not changed since the last 30 years (Trinidade 2005). In addition, it is believed to be much older although precise data are lacking (Schessl et al. in press). Most scientific activities during the first phase of

the project including all studies on *Parkia pendula* took place in this forest fragment. The 'Piedade' fragment is crossed by an unpaved road and harbors a small water reservoir (Figure 3). The fragments northern extension abuts on the sugar refinery; a small village is located near the fragments western border (Figure 3).

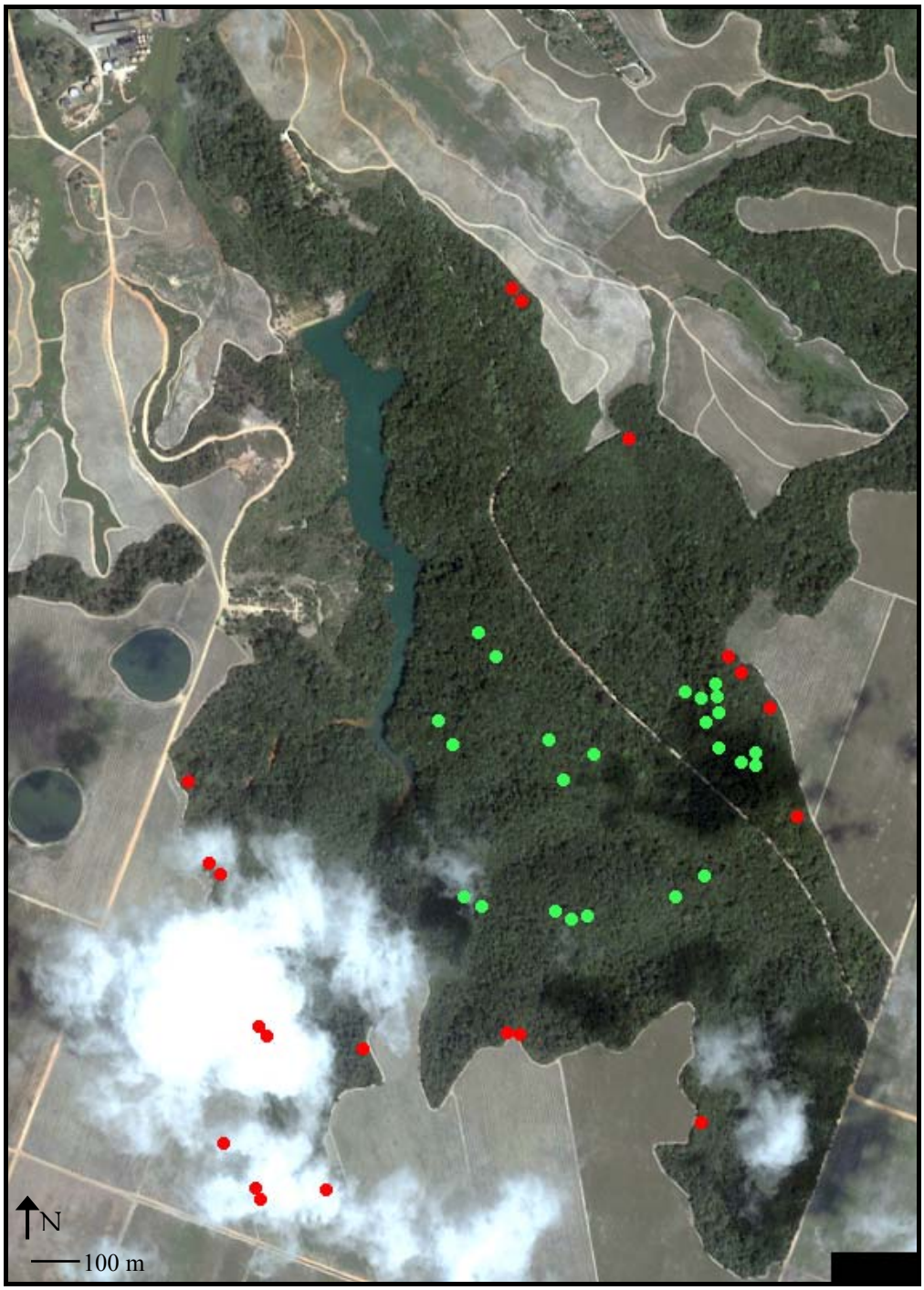

Figure 3 Satellite image (source: Ikonos, GeoEye, USA) of the forest fragment 'Piedade' with all 20 *P. pendula* adults in the edge zone (●) and all 24 adults in the forest interior (●).

The bedrock is a Tertiary conglomerate on beach-ridged terraces of the Barreiras group (Dominguez et al. 1990). The topsoil is a sandy to loamy red-yellow podzolic soil (Schessl et al. in press). Most of the fragment is located on a plain

plateau at an altitude of 110 m, whereas the northern part and the flooded valley have an altitude of approx. 30 m.

The mean height of the forest's close canopy is approx. 20 m; some emergent trees reach 35 m in height. Within the tree species, there is a tendency towards deciduousness during the dry season, wherefore this forest may be characterized as a semi-evergreen rainforest (Schessl et al. in press). The trees with the highest importance index values are *Thyrsodium schomburgkianum*, *Eschweilera ovata*, *Tapirira guianensis*, *Pogonophora schomburgkiana, Parkia pendula*, and *Protium heptaphyllum* (Silva 2005). The mean tree and liana density (dbh ≥ 5 cm) as well as the basal area of living trees are all significantly higher in the forest interior of the fragment 'Piedade' whereas the frequency of multi-trunked trees is higher in the forest edge zone (Schessl et al. in press, Silva 2005). A possible explanation for these results might be the firewood extraction by local people mentioned by Schessl et al. (in press). Those people use mainly the edge vegetation (pers. observ.). Furthermore, the farm workers regularly usee the forest edge zone as resting place during their lunch break (pers. observ.). This behavior results in some relatively open parts of the forest belt (Schessl et al. in press; 2.3) and edge zone surrounded by denser parts.

2.3. General Study Design

Most of the research presented in this study examined possible edge effects on different stages of the reproduction cycle of *Parkia pendula* (1.4). Generally, the total research of the research group dealt with edge effects during the first phase. Therefore, explicit definitions of the 'forest edge zone' and the 'forest interior' were needed to compare results. The lack of such definitions is one reason for the weak generalizations of edge effects in literature (Murcia 1995). Since the forest fragment 'Piedade' exists since several decades, the edge development led to a 'sealing', i.e., a development of dense vegetation at maintained edges (Harper et al. 2005). This 'sidewall' (Harper et al. 2005), 'Waldmantel' or 'forest belt' (Schessl et al. in press) may be several meters deep (Murcia 1995, Schessl et al. in press) and consists of core forest trees as well as pioneer trees, shrubs, and herbs (Schessl et al. in press). This forest belt is interpreted as a distinct habitat with a particular floristic composition and two sharply delineated borders; one outwards with the cart track (Appendix 2 a) and the other inwards with the adjacent forest vegetation, which lacks almost all ruderal and pioneer species of the forest belt (Schessl et al. in press). Therefore, in this study as well as in the whole project, the term 'forest edge zone' is used for the forest zone that directly borders the forest belt. The opposite term 'forest interior' is defined as forest with a minimum distance of 100 m to the nearest outer border of

forest belt since most edge effects are known to penetrate forests less than 100 m (Laurance et al. 2002).

Adult individuals of *P. pendula* had to be chosen for the studies on possible edge effects (1.4) in the forest interior as well as in the forest edge zone. Therefore, all 20 adult *P. pendula* individuals of the fragment 'Piedade' that were visible from the surrounding cart track were taken as edge zone individuals. The forest interior was perambulated until an equivalent number of trees was detected (Figure 3). To ensure that possible differences were caused by habitat effects rather than by morphometrical effects, the diameter at breast height (dbh) was calculated after measuring the circumference (Condit 1998) for every tree. Height was measured with a tape measure while climbing most of the trees. Additionally, crown area was calculated for most trees after measuring the crown expansion in eight directions (Mutke 2001) on the forest floor with an ultra sonic distance measuring unit (Vertex III, Haglöf Sweden AB, Sweden). Dbh, height, and crown area of the studied trees are listed in the appendix.

No significant differences were found in dbh, height, and crown area (Table 1) between the chosen individuals of the edge zone and the forest interior (Figure 3; Appendix 1). The median observed *P. pendula* tree had a crown area of 116.5 m², a total height of 19.8 m, and a diameter at breast height of 49 cm (Table 1). Therefore, possible differences cannot be explained with morphometrical differences of the two studied sub-populations but rather with habitat specific differences between the forest interior and the edge zone.

Table 1 Crown area, height, and dbh of all investigated adult *P. pendula* trees and p-values of differences between habitats.

	n	Median ± MAD	Min – Max	Mann-Whitney U	p
Crown area [m^2]	35	116.5 ± 29.5	48.0 – 804.5	135.0	0.633
Height [m]	36	19.8 ± 1.8	15.5 – 34.0	116.0	0.227
dbh [cm]	44	49.0 ± 9.7	28.4 – 140.1	184.0	0.187

3. Flower and Pollination Ecology of *Parkia pendula*

3.1. Abstract

The flower and pollination ecology of the common canopy tree *Parkia pendula* was studied in detail in a fragment of the Atlantic Forest in the northeastern Brazilian state of Pernambuco. The flagelliflorous capitula of this self-incompatible species consisted of 802 ± 34 hermaphroditic and fertile, as well as 263 ± 8 sterile and nectar-secreting flowers with an anthesis of a single night. The strong fruity odor was comprised of max. 11 compounds, most of them isoprenoids, of which *trans*-ß-ocimene was clearly dominating with up to 99.16%; no sulphur compounds were detected. Nectar volume was 7.4 ± 1.5 ml per capitulum with highest hourly production rates during early anthesis. Twenty-one amino acids were found in the hexose-dominated nectar with a mean sugar concentration of 15.9 ± 4.4%. The scent, as well as the nectar sugar and amino acid composition changed during anthesis, most probably due to flower wilting. The main pollinator was the large bat species *Phyllostomus discolor* with up to 466 visits per capitulum/night. This bat preferred capitula in clutter-free space, whereas a nectar-thief, the small *Glossophaga soricina*, visited obstructed capitula more frequently. The reproductive organs of *P. pendula* from capitulum buds to seed pods attracted a wide range of mammals. The conservational value of *P. pendula* as a possible keystone plant resource for the mammal fauna is discussed. Furthermore, differences in flower and pollination ecology of 'big-bat' flowers are compared with Neotropical 'glossophagine flowers'.

3.2. Introduction

Approximately 98–99% of all flowering plants in tropical lowland rainforests are pollinated by animals, mainly by insects (Bawa 1990), whereas only 0.5–1% of all Neotropical angiosperms depend on bats as pollen vectors (von Helversen 1993). There are more than 500 (Vogel 1969) and up to 1,000 plant species (Fleming 2003) in the Neotropics and about 100–200 species in the Brazilian Atlantic Forest, which are pollinated by bats, taking the data by Myers et al. (2000) as the basis for this calculation.

There are two different groups of flower-visiting bats in the Neotropics: highly specialized nectar-feeding bats of the Phyllonycterinae and Glossophaginae (von Helversen and Winter 2003), which have undergone morphological, physiological, and behavioral adaptations for economical nectar feeding (Tschapka and Dressler 2002), and secondly, larger and relatively unspecialized bats, mainly *Artibeus*, *Carollia*, *Phyllostomus*, and *Sturnira* (Dobat and Peikert-Holle 1985, von Helversen 1993, von Helversen and Winter 2003, Tschapka and Dressler 2002). In their extensive database, Dobat and Peikert-Holle (1985) list 136 Neotropical

plant species in 40 families that are known to be visited by bats. More than two third of these plants are visited solely by glossophagine bats (99 sp.), 13 species are listed to be visited by 'big bats' (von Helversen 1993) only, and 24 species were observed to be visited by bats of both groups (Dobat and Peikert-Holle 1985). Even if most of these plant-bat interactions have not been investigated deeply and many more cases of bat pollination have since been found (Geiselman et al. 2002 onwards, von Helversen 1993), it is obvious from this list that only relatively few plant species (27%) are available to unspecialized bats. The majority (73%) of chiropterophilous species in the New World is visited exclusively by specialized nectar bats (Dobat and Peikert-Holle 1985, Tschapka and Dressler 2002). This may be one reason for the focus of research on glossophagine bats during the last decades (von Helversen and Winter 2003). Therefore, it is comprehensible that descriptions of 'typical' interactions and morphological co-adaptations tend to focus on these more specialized species (Heithaus 1982).

The evolutionary relationship between bat-pollinated plants and their pollinators is a 'diffuse coevolution' (*sensu* Janzen 1980) because each group may include many species (Heithaus 1982) – maybe with the one recently discovered exception of *Centropogon nigricans*, which is exclusively visited by *Anoura fistulata* (Muchhala 2006). Nevertheless, chiropterophily is a well defined pollination syndrome, making it possible to predict the pollination by bats from herbarium specimens only (von Helversen and Winter 2003). However, a verification by direct observations is always required to prevent mistakes of judgment (Vogel 1958). The plant characters always related with chiropterophily are a) the nocturnal anthesis of b) large and c) strong blossoms (*sensu* Fægri and van der Pijl 1971). These blossoms are d) well exposed, e) often whitish or drab colored, produce large quantities of f) pollen and g) nectar, and have h) a strong, often fetid odor (e.g., Dobat and Peikert-Holle 1985, Fægri and van der Pijl 1971).

Glossophagines and the less specialized bats differ mainly in their size, capacity for tongue extension, and hovering ability (von Helversen and Winter 2003, Vogel 1969). These differences are crucial for their feeding behavior and nutritional demands, and should therefore be reflected in the characteristics of the visited flowers.

Parkia pendula is a widespread Neotropical tree species which is known to be visited by large, unspecialized bats, mainly *Phyllostomus discolor* (de Carvalho 1961, Hopkins 1984). The goal of this study was to score floral characters associated with chiropterophily in the context of unspecialized phyllostomid bats. This objective is approached by a combination of classical morphological investigations of blossoms (capitula) and flowers, and observations of anthesis and visitor behavior.

Furthermore, the temporal variation of nectar production, nectar sugar-, and amino acid composition, as well as the odor composition during anthesis were analyzed.

3.3. Material and Methods

3.3.1 Phenophases: developmental stages from buds to ripe pods

Six morphometrical variables were measured weekly to separate distinct developmental phases from buds to ripe pods in *P. pendula*. Following variables were observed, starting in September 2003: a) total length of the composed inflorescence, b) number of capitula per inflorescence, c) peduncle length, d) capitulum diameter, e) number of pods per capitulum, and f) mean pod length. The capitulum diameter was measured with a caliper to the nearest mm; all other variables were measured to the nearest cm using a tape measure. Additionally, the color of all generative structures was determined using the color-plates by Kornerup and Wanscher (1981). The morphometrical variables were observed at five inflorescences of two trees (trees D015 and D135; Appendix 1). Morphological terms were used following Hopkins (1986a).

3.3.2 Capitulum and flower morphology

Three flowering capitula of a single tree were collected on September 29, 2004 (tree D013; Appendix 1). Their exact number of fertile and nectar-secreting (sterile) flowers was counted using a stereomicroscope (Stemi 2000, Carl Zeiss AG, Germany) after several days of air-drying. High resolution images of the different flower types and their components were obtained by using a scanning electron microscope (SEM; Zeiss DSM 249, Carl Zeiss AG, Germany), after dehydration of the flower material in 70 and 100% isopropanol, critical point drying, and sputter coating with gold (Balzers Union Ltd., Liechtenstein).

3.3.3 Breeding system

To test for spontaneous self-pollination, five capitulum buds (phenophase 3; 4.4.1) of a single tree (tree D181; Appendix 1) were bagged with a self-made wire-framework covered with nylon fabric (Kearns and Inouye 1993) on September 20, 2003. The frameworks were attached on horizontally oriented branches and enclosed the capitula without touching them. Additional, five capitula were bagged with paper-bags during the last hours of the night on November 16, 2003, after measuring their nectar production (tree D128; Appendix 1). While measuring nectar, the fertile flowers were handled probably as roughly as the bats do, but visitation by animals was excluded. Therefore, at least some of the stigmas of every capitulum

were pollinated with pollen of the same flower or of flowers of the same capitulum (test for induced autogamy/geitonogamy).

The polyads of two anthers from five fertile flowers of four trees (trees D015, D125, D135, and D181; Appendix 1) each were counted as well as the ovula of these 20 flowers using a stereomicroscope (Stemi 2000, Carl Zeiss AG, Germany) for calculating the pollen per ovula ratio (P/O ratio) after Cruden (1977). For obtaining pollen numbers per flower, the number of polyads per flower was multiplied with 32, which is the common number of pollen grains per polyad in *Parkia* (Feuer et al. 1985).

3.3.4 Odor

Odor sampling

Odor was collected by headspace adsorption *in situ* from capitulum buds and flowering capitula (phenophases 3 and 4; 4.4.1) in the period from end of September to end of October 2004. Three flowering capitula of two trees (trees D015 and D125; Appendix 1) each were sampled. Additionally, samples were taken from four buds between 16:00 h and 20:00 h. Flower scent samples were taken three times per capitulum during anthesis (first sample between 18:00 h and 20:00 h, second between 22:00 h and 24:00 h, and third between 02:00 h and 04:00 h) to detect a possible temporal change in floral scent composition. In order to identify background contamination, a blank sample was always collected.

The capitula were enclosed in polyethylene bags (Toppits oven bags, Melitta Beteiligungs-GmbH & Co. KG, Germany) (Jürgens et al. 2006, Stewart-Jones and Poppy 2006). The scent-containing air was sucked through glass cartridges with a 1:1 by weight mixture of Tenax-TA, mesh 60-80, (Buchem bv, The Netherlands) and Carbopack X, mesh 40-60, (Supelco Corporation, USA) with a battery-operated membrane pump (Jürgens et al. 2003). The flow rate through the cartridges was approx. 150 ml · min^{-1}; sampling duration was 1 h per capitulum. Cartridges were conditioned before sampling by washing with 4 ml acetone and heating them for 30 min on a hotplate. The adsorbed scent substances were extracted with approx. 0.5 ml acetone into glass vials (2 ml clear vials with solid polypropylene screw caps with PTFE liner, Supelco Corporation, USA). These vials were kept in a freezer until floral scent analysis in Bayreuth, Germany.

Odor analysis

Analyses were carried out by Dr. Stefan Dötterl, Department of Plant Systematics, University of Bayreuth, Germany. The samples were analyzed on a Saturn 2000 mass spectrometer (MS) coupled to a Saturn 3800 gas chromatograph (GC) using a 1079

injector (all Varian Inc., USA) that had been fitted with the ChromatoProbe kit (Dötterl and Jürgens 2005). One µl of the samples was filled in a quartz vial, which was placed in the injector port by means of the ChromatoProbe. The injector split vent was opened (1/20) and the injector heated to 40°C to flush any air from the system. The split vent was closed after 2 min and the injector was heated at 200°C and held at 200°C for 4.2 min, after which the split vent was opened (1/10) and the injector cooled down. A ZB-5 column (5% phenyl polysiloxane) was used for the analyses (60 m long, inner diameter 0.25 mm, film thickness 0.25 µm, Phenomenex Inc., USA). Electronic flow control was used to maintain a constant helium carrier gas flow of 1.8 ml · min^{-1}. The GC oven temperature was held for 7 min at 40°C, then increased by 6°C · min^{-1} to 250°C and held for 1 min. The MS interface was 260°C and the ion trap worked at 175°C. The mass spectra were taken at 70 eV (in EI mode) with a scanning speed of 1 scan · sec^{-1} from m/z 30 to 350. The GC-MS data were processed using the Saturn software package 5.2.1 (Varian Inc., USA). Component identification was carried out using the NIST 02 mass spectral data base (NIST algorithm), or MassFinder 3.0, and confirmed by comparison of retention times with published data (Adams 1995). Identification of individual components was confirmed by comparison of both, mass spectrum and GC retention data, with those of authentic standards.

Data were analyzed using the repeated measures ANOVA and the Bonferroni post-hoc test of the software-package Statistica 6.0 (StatSoft Inc., 2001).

3.3.5 Nectar

Nectar quantity

Two different methods to measure the nectar production were used. Firstly, plastic funnels with a connected scaled-centrifuge tube (5 ml) were fixed directly below enclosed flowering capitula. The sampling equipment was always installed before 17:00 h. The amount of dropped nectar was read off at the tube in one-hour intervals. First metering was at 17:00 h, last at 03:00 h. This procedure was carried out during four nights at 12 capitula of a single tree (D128; Appendix 1) at the end of October 2003. Secondly, all nectar was removed every 15 min with a 1 ml-pipette directly at the nectar-secreting flowers. This was carried out at eight capitula of three trees (two at the end of October 2003, the remaining at the beginning of October 2004; trees D015, D125, and D128; Appendix 1).

The calculated median total nectar volume per capitulum was multiplied with the number of flowering capitula per tree (4.4.2) to obtain the approximate total nectar volume per tree and flowering period.

Because the nectar quantities were not normally distributed (Shapiro-Wilk-test of normality), the non-parametrical Mann-Whitney U test was used to detect differences between the two sampling methods instead and median and median absolute deviation (MAD) were used to specify the data location and dispersion. Calculations were carried out using SPSS for Windows 11.0 (SPSS Inc., 2001).

Nectar quality

Nectar sampling

Nectar was sampled with 5 µl micro capillaries (end-to-end capillaries, Hirschmann Laborgeräte GmbH & Co. KG, Germany) into microcentrifuge tubes (PP with screw cap (PE) with sealing cone, Brand GmbH & Co. KG, Germany) pre-filled with approx. 1 ml of ethanol (70%; HPLC-grade, Merck KGaA, Germany). Nectar was sampled this way on the hour between 17:00 h and 01:00 h at ten capitula of three trees (D013, D015, and D125; Appendix 1) during October 2004. After each sampling, the remaining nectar was removed from the capitula to ensure that only nectar produced during the specific hour was taken at the next sampling. The micro-tubes were stored in a freezer until HPLC analysis in Ulm. Disposable nitrile gloves were worn during the whole sampling and analyzing process to prevent contamination. Unfortunately, 58% of all samples leaked due to a material defect of the microcentrifuge tubes during storage and transportation and had to be removed from further analysis. Therefore, adequate temporal statistics like repeated measures ANOVA were not feasible.

Nectar analyses and calculations

The liquid content of the nectar samples had to be replaced by a known volume of water for the HPLC analyses. Therefore, the samples were vacuum-centrifugalized at 65°C (SpeedVac SC 110, Savant Instruments Inc., USA) until all liquidity vanished and only the nectar's solid components were left. These components were dissolved in 100 µl water (HPLC-grade) and purified by filtering (0.45 µm pore size, Acrodisc syringe filter with nylon membrane, 4 mm, Pall Corporation, USA). Fifty µl of this solution were necessary for the sugar analysis, 5 µl for the amino acid analysis.

Sugars

Following HPLC components were used: autosampler 717plus, pump 510, refractive index detector 410, and a column heater module (all Waters Corporation, USA). Isocratic separation was achieved using a 72:28 acetonitrile-water mix (Schmidt 1998) with a flow rate of 1.4 ml · min^{-1} and a high-performance carbohydrate column (4.6 mm x 250 mm, Waters Corporation, USA) with a guard column.

Operating temperature was 35°C. The mobile phase was degassed with helium 4.6 with a flow rate of 20 ml · min^{-1}. The system was monitored and data collected using the Millennium^{32} 3.0.5 software (Waters Corporation, USA). External standards for sucrose, fructose, and glucose (Merck KGaA, Germany) were run all 40 samples.

The HPLC output provided sugar concentrations in weight [µg] per sample volume [µl] for the single sugars. The concentrations had to be transformed into weight percent (sugar weight [µg] to total solution weight [µg], (w/w)) to provide comparability with published results (Bolten et al. 1979). This unit is identical with the °Brix scale commonly used by most refractometers (Bolten et al. 1979). Therefore, the sugar volume per sample volume [µl · $µl^{-1}$] had to be calculated by dividing the sugar weight by its density. The densities of the three occurring sugars are 1,580.5 µg · $µl^{-1}$ for sucrose, 1,600 µg · $µl^{-1}$ for fructose, and 1,562 µg · $µl^{-1}$ for glucose (Lide 1995). Adding the three sugar volumes resulted in the total sugar volume per sample volume. Subtracting this sugar volume from one resulted in the water volume [µl] per microliter of solution (with the simplified consideration of no further nectar components). The total solution weight [µg] per microliter of nectar was the multiplication of the water volume with 1,000 and the addition of the total sugar weight [µg]. Dividing the sugars weight by the total solution weight and multiplying the result with 100 resulted in the recommended weight percent unit.

Mean sugar production per capitulum and tree was calculated by multiplying the mean total sugar weight per milliliter nectar with the median nectar volume per capitulum and with the median nectar volume per tree (3.4.5). The caloric value of the nectar was calculated by multiplying the total sugars weight [g] with 15.91 kJ · g^{-1} (Winter et al. 1993).

The energy density (Tschapka 2004), which is the daily offered amount of nectar energy per hectare, was calculated by multiplying the nectar's mean caloric value per tree with the mean density of adult trees per hectare (6.4.2) and adjusting it with the median flowering pattern (4.4.1).

Amino acids

Amino acid analysis followed the AccQ•Tag method of the Millipore Corporation (1993). Samples (5 µl) were derivatized with AQC (6-aminoquinolyl-N-hydroxysuccinimidyl carbamate) in a borate buffer (without previous hydrolyzing). HPLC was performed using the following equipment: autosampler 717plus, 600E system controller, 470 scanning fluorescence detector, sat/in module, and a column heater module (all Waters Corporation, USA). Separation was achieved using an AccQ•Tag column (Novapak C_{18}, 3.9 mm · 150 mm, Waters Corporation, USA) with a guard column. The gradient profile by Schmidt (1998) was used for the three eluents (a: sodium acetate, triethylamine (TEA) buffered with phosphoric acid (pH

5.5), ethylene-diamine-tetraacetic acid (EDTA); b: acetonitrile; c: water) with a flow rate of 1 ml · min^{-1} at a operating temperature of 37°C. The mobile phase was degassed with helium 4.6 with a flow rate of 20 ml · min^{-1}. The system was monitored and data were collected using the Millennium^{32} 3.0.5 software (Waters Corporation, USA). An external standard for alanine, arginine, asparagine, cysteine, glutamine, glycine, histidine, isoleucine, lysine, methionine, phenylalanine, proline, serine, threonine, tyrosine, and valine (amino acid hydrolysate standard, Waters Corporation, USA) was run all 40 samples.

For comparing the concentration and composition of the nectar's amino acids between the different nectar samples, the coefficient of variation (Vc) and the Pearson correlation coefficient were computed following Gardener and Gillman (2001). However, the Vc could only be computed for the identified amino acids because the content could be determined only for these amino acids. The correlations of amino acid composition based on the chromatogram peak area of each amino acid because no unit was necessary for this analysis. Therefore, all detected amino acids could be used to calculate the correlation coefficients.

3.3.6 Capitulum visitors

The number of bat visits per capitulum was counted per min at four capitula during two nights from 17:00 h to 03:00 h. Three of these capitula were freely hanging, whereas one was localized next to a horizontally oriented branch. The observations were made at trees (D125, D181; Appendix 1) with crown access due to the single rope technique (Barker 1997). The distance to the observed capitula was 3–4 m. All observed capitula were well visible due to flashlight illumination (Duobelt LED 5, Petzl Sa., France). In all likelihood, the LED light and the near presence of man had no influence on the behavior and visiting frequency of the observed bats. Photographs (Nikon D 100, SB 29s Speedlight, (both Nikon Corporation, Japan) with a 28–300 mm F 3.5–6.3 lens (Tamron Corporation, Japan)) of capitulum visitors were made during additional observation nights to document the feeding behavior of the bats. Besides the bats, all other capitula-visiting vertebrates were recorded and their behavior was observed. Additionally, bats were captured with a mist net directly underneath the tree crown between the flowering capitula following the method of Tschapka (1998). Captured bats were identified by L.A. Menezes da Silva (University of Brasilia, Dept. of Zoology); forearm length of the captured individuals was measured with a caliper. The bats' weight was determined with a spring balance and attached polyads were collected with adhesive tapes (Elmqvist et al. 1992) that were mounted on microscope slides afterwards. All bats were released unharmed after measurements.

3.4. Results

3.4.1 Phenophases: developmental stages from buds to ripe pods

Eleven distinct phenophases could be easily identified in the field from young inflorescence buds to open pods (Figure 4; Table 2) and are introduced in the following. Because the inflorescence abortion rate was very high during the first five weeks of bud ripening, morphometrical variables were measured starting during the 6th week of inflorescence development. Nevertheless, there were clear differences between the inflorescence buds of the first two weeks compared with older ones. During the first two weeks (phenophase 1, initial phase), the inflorescence bracts opened. The whole inflorescences were very compact (<5 cm total length) and all capitulum buds were still completely enclosed by capitular bracts (Figure 4 a). Phenophase 2 (elongating phase) was characterized by the elongating of the primary axes of the compound inflorescences whereas the peduncles were still relatively short. The number of capitulum buds (and peduncles) decreased dramatically (Table 2) during this five-weeks-lasting period. The capitular bracts of the remaining capitulum buds opened (Figure 4 b). The final total inflorescence and peduncle length as well as the final number of capitula per inflorescence (Table 2; Figure 4 c, d) was reached during the pre-flowering phase (phenophase 3). The capitulum buds started emitting odor during the late pre-flowering phase. The following flowering phase (phenophase 4) comprised the day before the one night of flowering as well as the following days until all unfertilized flowers were aborted (Figure 4 e-g). Due to the open flowers, the capitulum diameter was clearly larger than before (Table 2). Opening started around noon of the day before the flowering night (i.e., ca. 30 h before start of the nectar production) when the subtending bracts of the nectar-secreting flowers lifted slightly and the styles elongated, wherefore the capitula looked somehow linty (Figure 4 e). The fertile flowers opened 24 h later, i.e., around noon before the flowering night. The well-exserted bright red colored anthers and the apical part of the filaments were the source of the capitula's red color. The time of anther opening corresponded always with the start of the nectar production around dusk. After anther opening the red color of the capitula became a slightly yellowish tone due to the openly presented yellow-colored polyads. Additionally, large nectar drops accumulated at the styles of the nectar-secreting flowers soon after dusk (Figure 4 f; 3.4.5.). The pale styles of the fertile flowers elongated between 20:00 h and 21:00 h and exceeded the anthers. The anthers were getting darker with proceeding time. Therefore, the capitula's color and brightness changed from bright red via red with a yellowish tone to dark purple-red during the one night of anthesis.

Most flowers aborted during the next three to four days, only 50 to 100 flowers remained at the olive-green receptacle (Figure 4 g). A small fraction of these flowers developed into small, olive-green pods (phenophase 5, reduction phase; Figure 4 h), and just every seventh of these latter proceeded its development (Table 2). These pods grew strongly during the following week of phenophase 6 (growth phase; Figure 4 i). The color of the pods changed to reddish-brown (Table 2) during the growth phase and turned deep green thereafter in phenophase 7 (unripe phase). The fruits reached their final length and final number per capitulum in phenophase 7 (Table 2). After three weeks, they entered phenophase 8 with producing a very sticky exudate, especially at the thickened ventral sutures (Figure 4 j). This gum-producing phase (phenophase 8) lasted two weeks before gum production stopped and the pods began to dry out. The pre-dispersal phase (phenophase 9) lasted for one to two weeks. The pods were dry and dark and the gum was still attached. The following dispersal phase (phenophase 10) lasted for several weeks, depending on the amount of precipitation. Although the pods were open, a huge number of seeds remained on the pods glued to the very sticky exudate (Figure 4 k) or still being connected with the pod by their funicles. The pods often remained for several months still attached on the tree after releasing all the seeds (post-dispersal phase, phenophase 11).

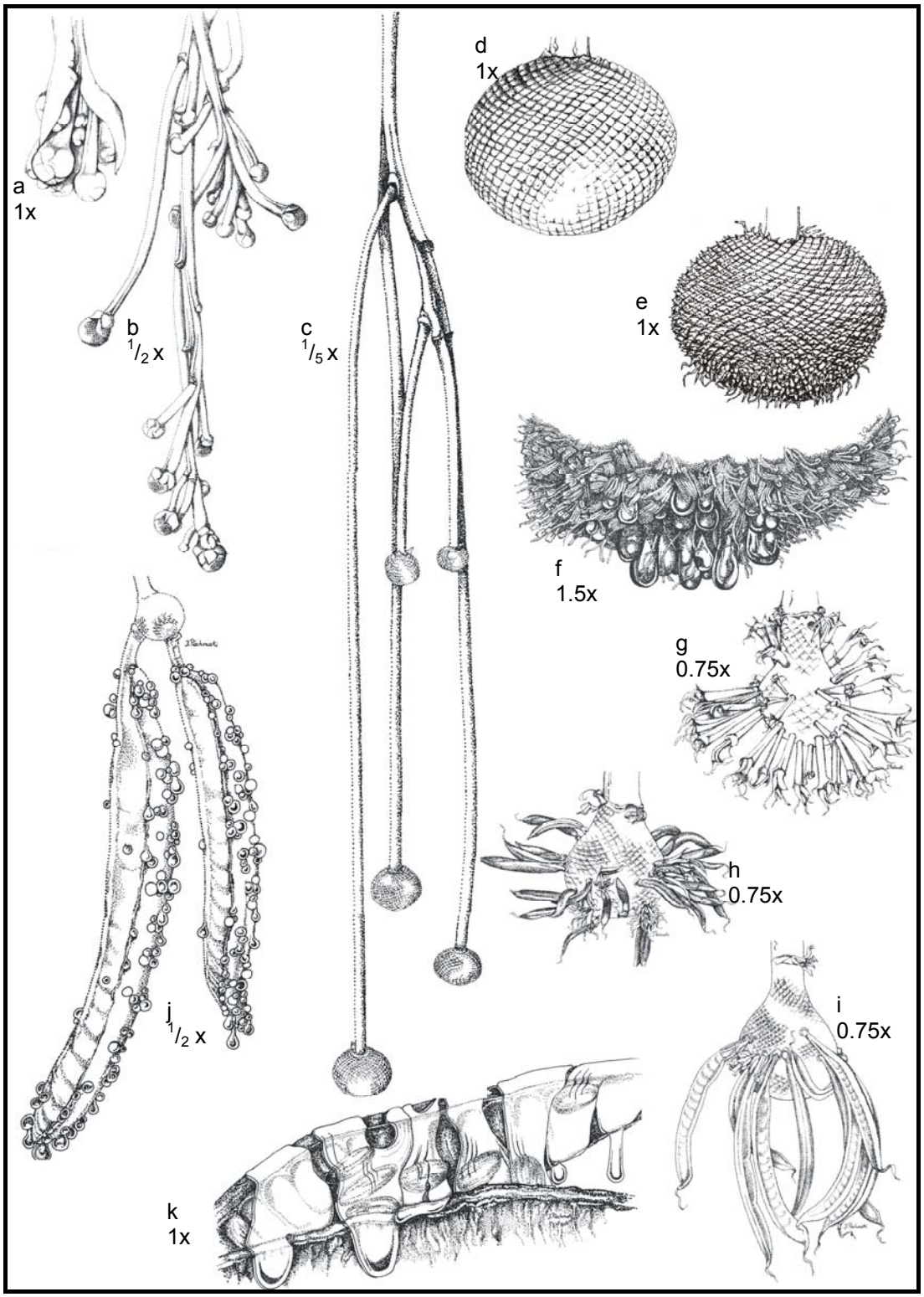

Figure 4 Phenophases of *P. pendula* from inflorescence bud to mature pod. a: initial phase; b: elongating phase; c, d: pre-flowering phase; e: early flowering phase; f: detail of a flowering capitulum with nectar drops at the sterile flowers; g: post-flowering phase; h: reduction phase; i: growth phase; j: gum-producing phase; k: detail of an open mature pod (Illustrations by J. Piechowski after photographs).

Table 2 Morphometrical variables (mean ± SD) and color of the buds, inflorescences, capitula, flowers, and pods during the different phenophases of *P. pendula*.

Week	Inflorescence length [cm]	No. of capitula / inflorescence	Peduncle length [cm]	Capitulum diameter [cm]	No. of pods / capitula	Pod length [cm]	Color of bud / flower / pod	Phenophase
1	-	-	-	-	-	-	olive-green	Initial (1)
2	-	-	-	-	-	-	olive-green	
3	-	-	-	-	-	-	olive-green	
4	-	-	-	-	-	-	olive-green	
5	-	-	-	-	-	-	olive-green	Elongating (2)
6	32.6 ± 17.8	15.8 ± 6.2	-	-	-	-	olive-green	
7	58.6 ± 18.2	14.2 ± 3.1	-	-	-	-	olive-green	
8	93.2 ± 20.6	2.4 ± 1.1	41.7 ± 13.0	1.6 ± 0.3	-	-	olive-green	
9	115.2 ± 13.5	1.8 ± 0.8	71.3 ± 12.7	2.3 ± 0.3	-	-	olive-green	Pre-flowering (3)
10	118.8 ± 10.8	1.6 ± 0.9	73.7 ± 12.1	3.2 ± 0.1	-	-	olive-green	
11	118.2 ± 10.4	1.6 ± 0.9	73.1 ± 12.3	4.1 ± 0.2	-	-	bright red	Flowering (4)
12	117.6 ± 10.6	1.6 ± 0.9	73.0 ± 12.4	1.9 ± 0.1	35.7 ± 26.2	2.2 ± 1.3	olive-green	Reduction (5)
13	117.2 ± 11.3	1.4 ± 0.9	72.7 ± 12.4	2.0 ± 0.2	21.9 ± 22.6	4.4 ± 2.0	olive-green	
14	117.8 ± 11.2	1.4 ± 0.9	72.9 ± 12.1	2.1 ± 0.2	5.4 ± 3.9	13.0 ± 4.8	reddish-brown	Growth (6)
15	117.0 ± 11.0	1.4 ± 0.9	72.6 ± 12.2	2.0 ± 0.2	4.9 ± 2.9	18.1 ± 3.3	deep green	
16	117.8 ± 11.6	1.4 ± 0.9	72.9 ± 12.3	2.1 ± 0.2	4.4 ± 2.4	19.3 ± 1.8	deep green	Unripe (7)
17	117.0 ± 11.5	1.4 ± 0.9	72.6 ± 12.2	2.0 ± 0.2	4.3 ± 2.3	19.4 ± 2.0	deep green	
18	117.6 ± 10.9	1.4 ± 0.9	72.6 ± 12.2	2.1 ± 0.2	4.3 ± 2.3	19.3 ± 2.3	deep green	Gum-producing (8)
19	117.6 ± 11.8	1.4 ± 0.9	72.6 ± 11.7	2.0 ± 0.2	3.9 ± 2.2	19.5 ± 2.3	deep green	

3.4.2 Capitulum and flower morphology

Three quarters of the total number of 1,065 ± 36 (mean ± SD) flowers per capitulum were fertile, only one quarter was composed of sterile, nectar-secreting flowers (Table 3). All fertile flowers were hermaphroditic, no male flowers were found.

Table 3 Mean number of fertile and nectar-secreting flowers per capitulum of *P. pendula*.

	n	Mean ± SD	Mean % of total	Min – Max
Fertile	3	802 ± 34	75.3	773 – 839
Nectar-secreting	3	263 ± 8	24.7	256 – 272
Total	3	1,065 ± 36	100.0	1,029 – 1,100

The two flower types had the same length but due to the nectar-secreting tissue, the nectar-secreting flowers were thicker towards the base (Figure 5). Both types contained anthers with polyads and an ovary with ovules. However, the sexual organs of the nectar-secreting flowers were slightly modified when compared to the fertile ones. The filaments were much shorter and curled (Figure 5 d) so that the anthers did not exsert the corolla whereas the style rose above the flower tube (Figure 5 c). Additionally, the ovary was much shorter since it was limited to the upper third of the flower due to the voluminous nectar-secreting tissue at the base of the flowers that was lacking in the fertile flowers (Figure 5 a, d).

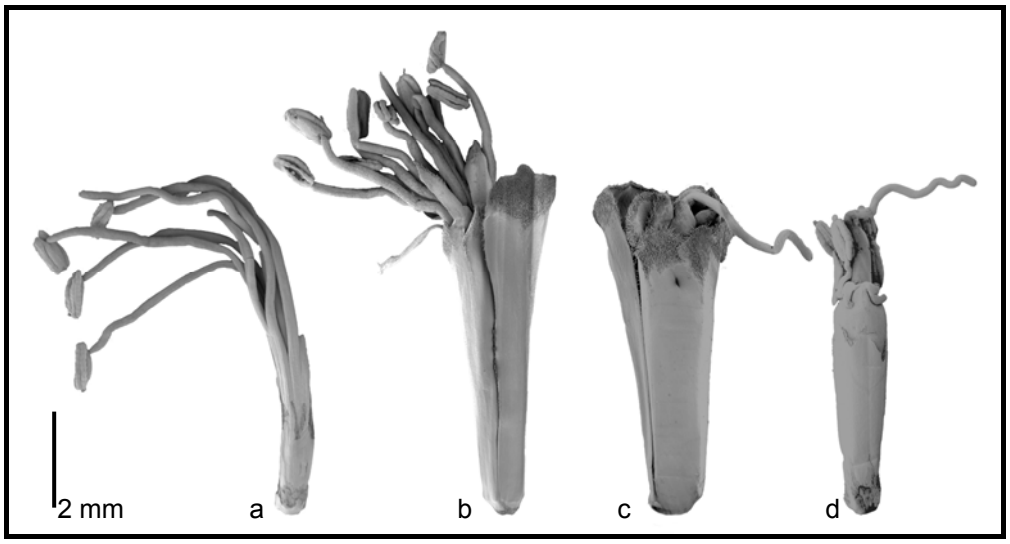

Figure 5 Fertile and nectar-secreting flowers of *P. pendula*. a: fertile flower without bract, calyx and corolla; b: total fertile flower; c: total nectar-secreting flower; d: nectar-secreting flower without bract, calyx and corolla (twisting of filaments and styles is caused by the preparation for SEM).

The pollen sacs of the fertile flowers dehisced longitudinally and presented two rows of polyads (Figure 6 c). These large yellow polyads (Figure 6 e) were visible even in closed pollen sacs due to the protrusions they caused in the walls of the

thecae (Figure 6 a, b). A dehiscence of the pollen sacs of the nectar-secreting flowers was never observed. The pink colored anther glands (Figure 6 d) dropped off the anthers very easily (compare anthers in Figure 5).

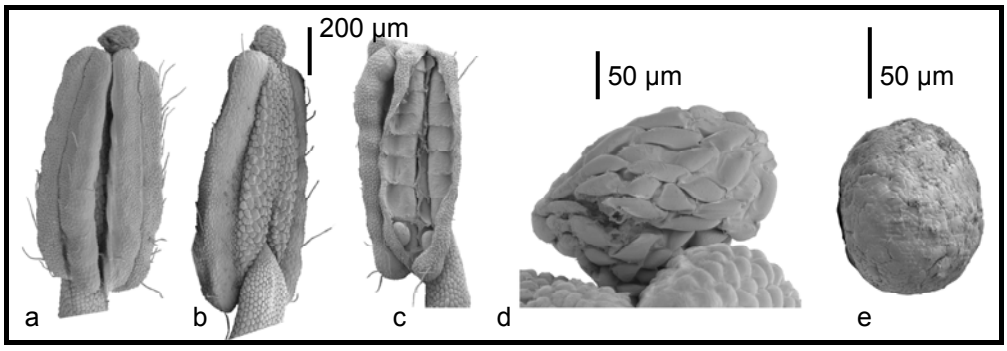

Figure 6 Anther, anther gland, and polyad of *P. pendula*'s fertile flowers. a–c: anther, a: ventral, b: dorsal, c: open thecae with presented polyads; d: anther gland; e: polyad.

The number of nectar-secreting flowers per total flowers found in *P. pendula* was quite high compared with previous counts of Amazonian populations and compared with other *Parkia* species (Table 4). Nevertheless, there is a clear correlation between the numbers of the different flower types per capitulum in *Parkia* (Figure 7 a). In general, (6) 10-20 (25)% of all flowers per capitulum are nectar-secreting flowers. This range displays the differences between species as well as the intraspecific differences between populations as detected in *P. pendula*, *P. discolor*, and *P. gigantocarpa* (Table 4). However, the wide range of total flowers per capitulum among the different species, ranging from 1,065 flowers per capitulum in *P. pendula* up to 4,390 in the African *P. filicoidea*, does not correlate with the size of the capitula (Figure 7 b).

Table 4 Capitulum length and number of nectar-secreting and total flowers per capitulum of different bat-pollinated *Parkia* species.

Species	Region	Capitulum length [cm]	Nectar-producing flowers / total flowers (%)
P. bicolor	West Africa	5.5 – 8 [1] 5.1 – 8.9 [2]	140 / 1,500 [1] (9) 329 / 2,890 [2] (11)
P. biglobosa	West Africa	4.5 – 7 [1]	261 / 2,552 [1] (10)
P. cachimboensis	Amazonia	5 – 6 [4]	193 / 1,122 [7] (17)
P. decussata	Amazonia	5.5 – 7.5 [4] 6.9 – 7.2 [5]	220 / 1,797 [7] (12)
P. discolor	Amazonia	4.5 – 6.5 [4]	260 / 1,650 [9] (16) 155 / 2,492 [5] (6)
P. filicoidea	Central Africa	6 – 9 [1]	621 / 4,390 [7] (14)
P. gigantocarpa	Amazonia	23 [3] 15 – 21.5 [4] 18 – 20 [5]	400 / 1,600 [3] (25) 251 / 1,830 [4] (14)

Table 4 cont.

P. ingeiflora	Amazonia	6.5 – 8.5 [4] 8.0 – 8.5 [5]	406 / 3,152 [7] (13)
P. nitida	South America	4.5 – 8 [4] 4.6 – 5.6 [5]	171 / 1,529 [7] (11)
P. panurensis	Amazonia	4.5 – 7 [4] 5.5 – 6.3 [5]	253 / 2,084 [7] (12)
P. pendula	Central & South America	3 – 3.4 [5]	187 / 1,290 [5] (14) 263 / 1,065 [6] (25)
P. speciosa	Southeast Asia	7 [8] 5.4 – 6.7 [10]	649 / 3,537 [7] (18) 459 / 2,165 [10] (21)
P. versteeghii	New Guinea	4.7 – 6 [10]	235 / 1,900 [10] (12)

[1] = Hopkins (1983a); [2] = Grünmeier (1990); [3] = de Carvalho (1960); [4] = Hopkins (1986a); [5] = Hopkins (1984); [6] = present work; [7] = Hopkins (1981); [8] = van der Pijl (1936); [9] = Vogel (1968); [10] = Hopkins (1994)

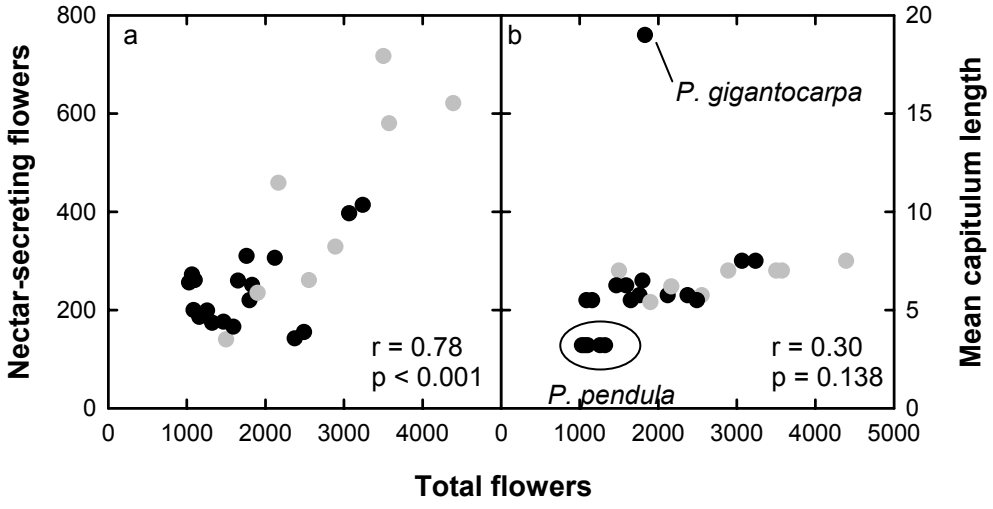

Figure 7 Total flowers *vs.* (a) nectar-secreting flowers and (b) mean capitulum length of the *Parkia* species mentioned in Table 4. Gray: Old World species, black: New World species.

3.4.3 Breeding system

Neither the entirely bagged capitula nor the self-pollinated capitula set fruit. All ten capitula wilted and were aborted within three to four weeks after flowering. The mean number of polyads (Figure 6 e) and ovula were quite stable with 33.3 ± 2.5 polyads per anther and 27.1 ± 2.7 ovula per ovary resulting in a mean P/O ratio of 397.3 ± 60.2 (Table 5).

Table 5 Ratios (mean ± SD) of polyads, pollen, and ovules of fertile flowers of *P. pendula* (n = 20).

Polyads/anther	Polyads/flower	Ovula/flower	Polyads/ovulum	Pollen/ovulum
33.3 ± 2.5	332.5 ± 24.9	27.1 ± 2.7	12.4 ± 1.9	397.3 ± 60.2

The mean number of polyads per capitulum was 266,665, taking only the mean number of fertile flowers (Table 3) into account since no dehiscence of the pollen sacs of the nectar-secreting flowers occurred (3.4.2).

3.4.4 Odor

Flowering trees of *P. pendula* emitted a strong fruity odor comparable to fermenting fruits, which was even detectable on the forest floor beneath the crown.

All samples of capitulum buds contained α-pinene and geranyl acetone (Table 6), which were only slightly present in the flower bouquets (Table 7). Only one of the four samples of capitulum bud odor contained additionally four more monoterpenes (Table 6).

One alcohol, one compound of an unknown class, and nine different isoprenoids were found in the floral odor of all open flowers (Table 7). Just three of these compounds have not been detected in all six sampled capitula (myrcene, geranial and 4,8-dimethyl-1,3,7-nonatriene). The dominating compound in all samples was *trans*-β-ocimene. The relative amount of this main compound changed significantly during anthesis (Table 8). Its relative amount increased from 54.91% during the first time interval to 84.04% and 90.87% in the second and third interval, respectively (Table 7). Other compounds decreased significantly during anthesis (cis-3-hexen-1-ol, neral and slightly not significant the unknown monoterpene oxide) or even disappeared (neral, linalool, unknown compound; Figure 8).

Table 6 Odor composition of *P. pendula* capitulum buds (n = 4). Numbers in parentheses indicate the number of buds in which a given compound was detected, if not found in all capitula. Compounds are listed according to relative retention time order.

	Mean % prod.	Min – Max	
Isoprenoids			
Monoterpene hydrocarbons			
α-pinene	48.79	32.47 – 74.09	
sabinene	1.44	0 – 5.76	(1)
β-pinene	5.04	0 – 20.16	(1)
myrcene	2.19	0 – 8.75	(1)
β-phellandrene	2.43	0 – 9.71	(1)
Irregular terpenes			
geranyl acetone	40.11	4.25 – 67.53	
Total number of compounds		6	

Table 7 Scent compounds of flowers of *P. pendula* and their changes during anthesis. Numbers in parentheses indicate the number of capitula per time interval in which a given compound was detected, if not found in all capitula; tr = trace amounts (< 0.1%).

	18:00 – 20:00 (n = 6)			22:00 – 00:00 (n = 6)			02:00 – 04:00 (n = 5)		
	Mean % prod.	Min - Max		Mean % prod.	Min - Max		Mean % prod.	Min - Max	
Fatty acid derivatives									
Alcohols									
cis-3-hexen-1-ol	15.47	0 – 27.73	(5)	1.38	0 – 6.65	(4)	0.16	0 – 0.76	(2)
Isoprenoids									
Monoterpene hydrocarbons									
α-pinene	2.22	0 – 6.44	(3)	0.64	0 – 1.71	(4)	1.14	0 – 3.90	(4)
myrcene							0.72	0 – 2.71	(3)
cis-β-ocimene	1.43	0 – 2.91	(4)	6.13	3.70 – 11.26		4.72	0.84 – 7.70	
trans-β-ocimene	54.91	43.34 – 84.52		84.04	68.80 – 91.56		90.87	83.50 – 99.16	
neral	7.58	5.19 – 15.48		0.29	0 – 1.67	(2)			
geranial	4.16	0 – 8.48	(4)	0.30	0 – 1.78	(1)			
Oxygenated terpenes									
linalool	4.38	0 – 8.78	(5)	2.38	0 – 6.73	(4)			
unknown monoterpene oxide	5.66	0 – 12.19	(5)	4.12	0 – 10.20	(5)	tr	0 – 0.41	(1)
Irregular terpenes									
4,8-dimethyl-1,3,7-nonatriene	0.18	0 – 1.08	(1)	tr	0 – 0.53	(1)	tr		(1)
geranyl acetone	1.75	0 – 7.66	(2)	0.13	0 – 0.81	(1)	2.29	0 – 5.31	(4)
Unknown	2.25	0 – 5.25	(5)	0.50	0 – 1.49	(3)			
Total number of compounds	11			11			8		

Table 8 Results of the repeated measures ANOVA for all eight odor compounds that occurred in all sampled capitula of *P. pendula* during anthesis. Bold compounds changed significantly during anthesis.

Compound	df	SS	MS	F	p
***cis*-3-hexen-1-ol**	**2**	**725.94**	**362.97**	**6.26**	**0.023**
α-pinene	2	11.59	5.80	1.42	0.296
cis-β-ocimene	2	60.78	30.39	3.96	0.064
***trans*-β-ocimene**	**2**	**3,839.21**	**1,919.60**	**9.79**	**0.007**
neral	**1**	**159.29**	**159.29**	**30.37**	**0.003**
linalool	1	11.99	11.99	0.90	0.386
unknown monoterpene oxide	2	95.46	47.73	3.63	0.075
unknown	1	9.22	9.22	3.06	0.141

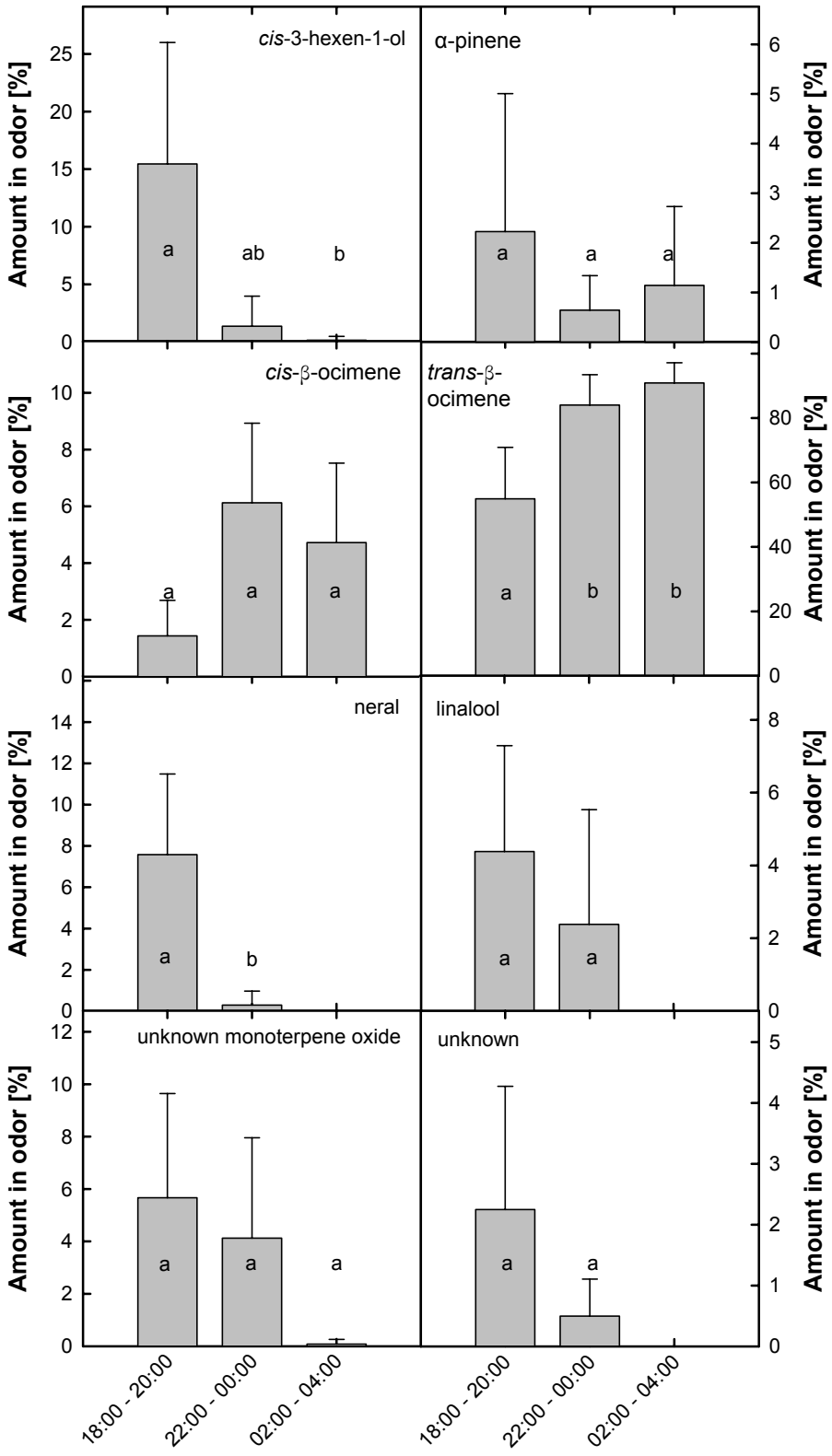

Figure 8 Change of relative amounts in odor of all eight odor compounds that occurred in all sampled capitula of *P. pendula* during anthesis. Different letters indicate significant differences between intervals as calculated by the repeated measures ANOVA with the Bonferroni post-hoc test ($p < 0.05$). Bars represent means ± SD.

3.4.5 Nectar

Nectar quantity

The total nectar volume per capitulum and night measured by removing the nectar with a pipette ranged from 4.5 ml to 21.0 ml. Nectar volume measured with the funnel method, i.e., measuring the dropped nectar, ranged from 5.8 ml to 15.1 ml (Table 9). No significant differences in nectar volume between removal and non-removal were detected (Mann-Whitney U: 36.0; p = 0.384).

Nectar production was largest right after the start of nectar production (18:00 h) (Figure 9). The production decreased slightly until 22:00 h and more rapidly thereafter until the end of production at 03:00 h (Figure 9).

Table 9 Total nectar volume per capitulum of *P. pendula*.

	n	Median ± MAD [ml]	Min – Max [ml]
Funnel	12	6.7 ± 0.8	5.8 – 15.1
Pipette	8	8.9 ± 1.4	4.5 – 21.0
Total	20	7.4 ± 1.5	4.5 – 21.0

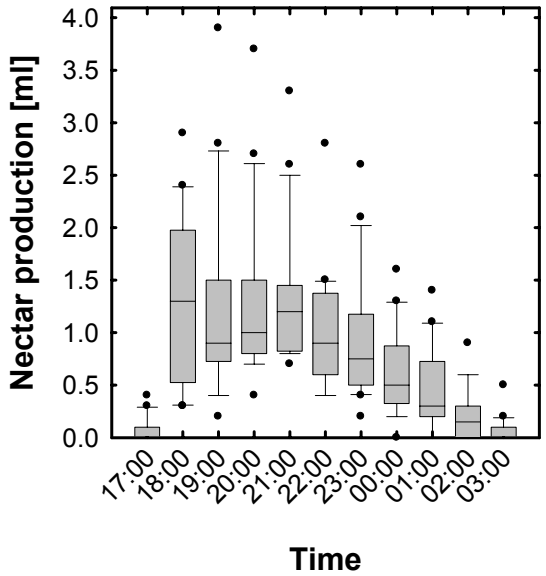

Figure 9 Temporal variation in nocturnal nectar production of *P. pendula* (n = 20) including both measuring methods (funnel and pipette; see text for more information).

The calculation of the total nectar volume per tree (Table 10) shows the large amounts of nectar offered per tree and flowering period with quantities up to 42 l per tree. Enormous differences in the number of capitula per tree between and within the two habitats (4.4.2) were the reason for the wide range of produced nectar per tree.

Table 10 Total nectar volume per *P. pendula* tree in both habitats.

	n	Median ± MAD [ml]	Min – Max [ml]
Edge	20	9,435 ± 8,397	0 – 27,750
Interior	4	1,598 ± 1,630	0 – 42,180
Total	44	6,386 ± 6,131	0 – 42,180

Nectar quality

Sugars

Three sugars were found in *P. pendula* nectar, the two hexoses fructose and glucose and the disaccharide sucrose. The nectar sugar concentration was very variable.

Table 11 Nectar sugar composition of *P. pendula* in percent (weight/total weight) and sugar ratio (s: sucrose; g: glucose; f: fructose).

Time	Sugars	n	Weight/total weight [%]		Sugar ratio [s/(g+f)]	
			Mean ± SD	Min – Max	Mean ± SD	Min – Max
17:00 h & 18:00 h	Fructose	4	10.0 ± 2.6	7.0 – 13.1	0.26 ± 0.14	0.04 – 0.41
	Glucose	4	6.3 ± 1.4	4.2 – 7.4		
	Sucrose	4	3.2 ± 2.1	0.4 – 5.3		
	Total	4	19.5 ± 5.6	11.5 – 23.7		
19:00 h & 20:00 h	Fructose	11	8.2 ± 2.3	5.5 – 11.2	0.13 ± 0.12	0.00 – 0.38
	Glucose	11	5.0 ± 1.2	3.1 – 7.1		
	Sucrose	11	2.1 ± 1.9	0.0 – 5.0		
	Total	11	15.2 ± 4.2	8.6 – 21.6		
21:00 h & 22:00 h	Fructose	8	8.2 ± 2.0	6.5 – 10.9	0.02 ± 0.02	0.00 – 0.07
	Glucose	8	5.0 ± 1.3	3.6 – 6.6		
	Sucrose	8	0.4 ± 0.3	0.0 – 0.7		
	Total	8	13.6 ± 3.4	10.6 – 18.0		
23:00 h & 24:00 h	Fructose	8	9.2 ± 2.4	5.2 – 12.0	0.04 ± 0.05	0.00 – 0.13
	Glucose	8	5.9 ± 2.0	2.6 – 8.4		
	Sucrose	8	0.9 ± 1.1	0.0 – 2.7		
	Total	8	16.1 ± 5.3	7.7 – 23.1		
01:00 h & 02:00 h	Fructose	7	10.3 ± 2.7	7.6 – 13.6	0.02 ± 0.02	0.01 – 0.05
	Glucose	7	6.2 ± 1.4	4.6 – 7.8		
	Sucrose	7	0.5 ± 0.3	0.1 – 0.7		
	Total	7	17.0 ± 4.2	12.4 – 22.1		
Total	Fructose	38	9.2 ± 2.4	5.1 – 14.0	0.09 ± 0.12	0.00 – 0.41
	Glucose	38	5.6 ± 1.5	2.6 – 8.4		
	Sucrose	38	1.2 ± 1.5	0.0 – 5.3		
	Total	38	15.9 ± 4.4	7.7 – 23.7		

It was highest right after the start of nectar production, decreased until 22:00 h, and increased until the end of nectar production again (Table 11, Figure 10). This temporal pattern in total sugar concentration was a result of the temporal progression of the two major components, fructose and glucose. The fructose concentration declined from 10.0% ± 2.6% to 8.2 ± 2.0% and increased afterwards again to 10.3% ± 2.7%, while the glucose concentration started with 6.3% ± 1.4%, decreased to 5.0% ± 1.3% and increased to 6.2% ± 1.4% thereafter (Table 11). The sucrose concentration did not follow this temporal pattern. It decreased from 3.2% ± 2.1% at the first measurements to 0.5% ± 0.3% at the end of nectar production. The ratio by weight of sucrose to the hexoses changed due to the distinct decrease of sucrose from 0.26 ± 0.14 at the start of nectar production to 0.02 ± 0.02 at the end of production (Table 11). *P. pendula* nectar was therefore changing its nectar category (*sensu* Baker and Baker 1990) during anthesis from hexose-rich (sugar ratio 0.10–0.49) to hexose-dominated (< 0.10).

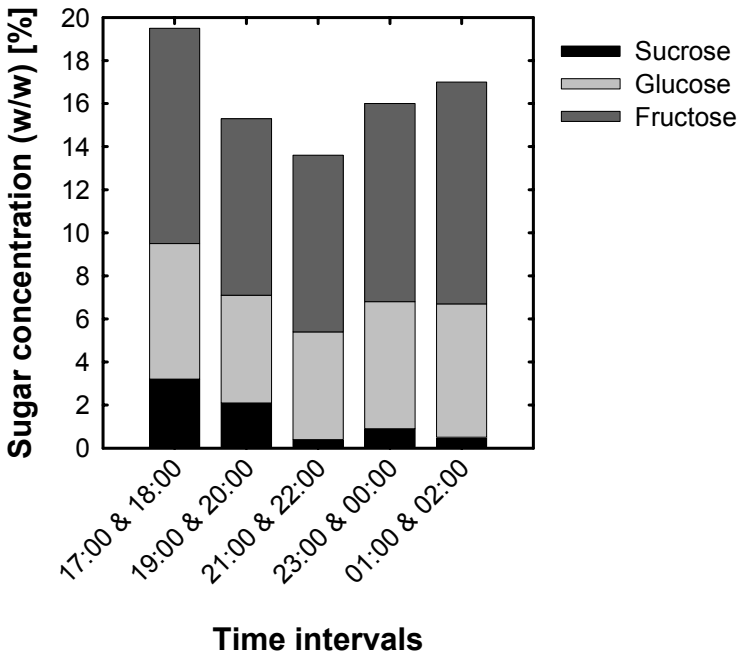

Figure 10 Temporal pattern of the mean *P. pendula* nectar sugar composition and concentration in percent (weight/total weight).

The total sugar weight per nectar volume was 170.5 ± 49.9 mg · ml^{-1} (mean ± SD) with an energy content of 2.7 ± 0.8 kJ · ml^{-1}. Multiplication with the mean nectar production per capitulum resulted in 1.3 ± 0.4 g sugar equivalent or 20.0 ± 7.2 kJ per capitulum. The calculated sugar yield per tree varied from 0 to over 7 kg (Table 12) due to the wide range of numbers of capitula per tree within and between habitats (4.4.2).

Table 12 Sugar equivalent and nectar energy per *P. pendula* tree.

	Sugar equivalent [g/tree]		Energy [kJ/tree]	
	Median ± MAD	Min – Max	Median ± MAD	Min – Max
Edge	1,609 ± 1,512	0 – 4,731	25,475 ± 23,947	0 – 74,925
Interior	272 ± 289	0 – 7,192	4,315 ± 4,574	0 – 113,889
Total	1,089 ± 1,089	0 – 7,192	17,242 ± 17,414	0 – 113,889

The roughly calculated daily energy density for a standardized flowering period of three weeks (4.4.1) and the observed population structure (6.4.2) showed during its peak in the second week a median of 3,100 ± 3,130 kJ $ha^{-1}d^{-1}$ (Table 13). This is the potentially available nectar energy per night and hectare offered for pollinating animals.

Table 13 Energy density during a standardized flowering pattern of *P. pendula*.

	Energy density [kJ • ha-1 • d^{-1}] Median ± MAD
1st week	1,550 ± 1,565
2nd week	3,100 ± 3,130
3rd week	1,550 ± 1,565

Amino acids

A total number of 21 different amino acids was found in the nectar of *P. pendula*. Only eleven of these could be identified due of the restricted number of standards available during the analysis. The qualitative visualizing of these 21 amino acids during different flower ages reveals different temporal production patters (Figure 11): alanine and proline were present in nearly all and the unidentified amino acids u3–u7 in most samples. Other amino acids were exclusively – or almost exclusively – produced during the first hours of flower anthesis, like arginine and threonine, or towards its end, like serine and valine.

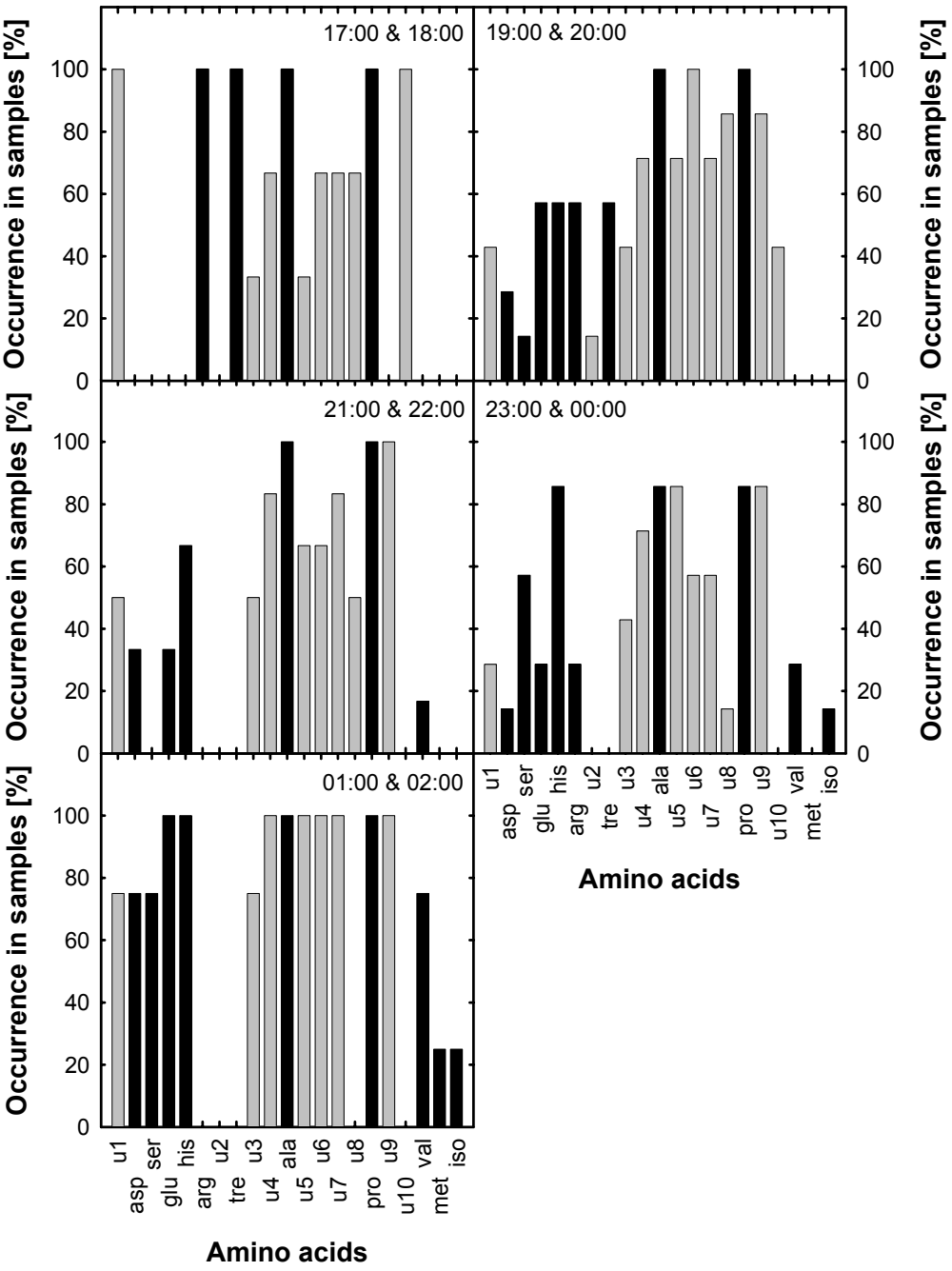

Figure 11 Temporal changes of amino acid composition of *P. pendula* nectar. u1–u10 (light bars): unidentified amino acids.

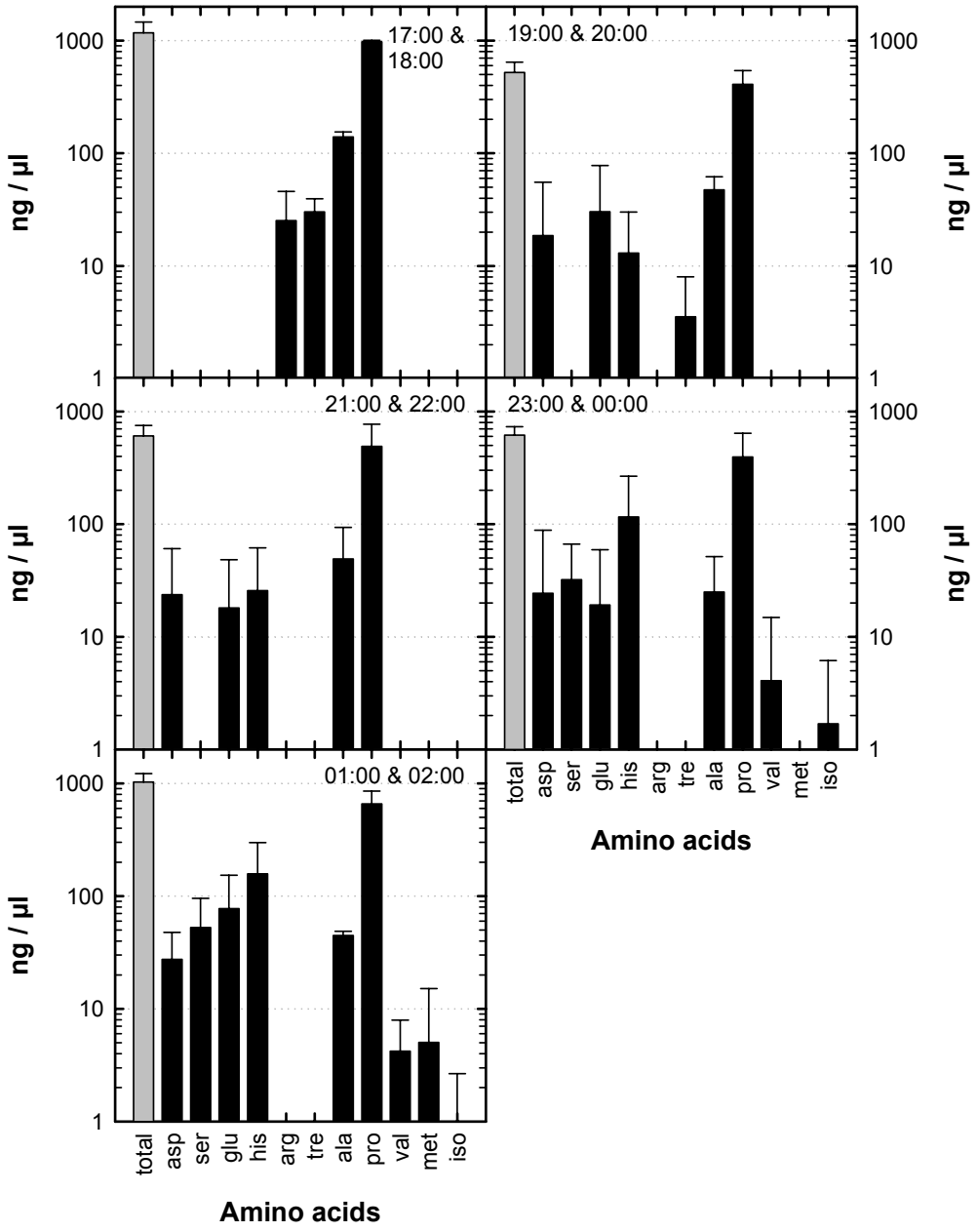

Figure 12 Temporal changes of the identified amino acid quantities (mean ± SD) of *P. pendula* nectar.

Quantitative analyses were possible for the identified amino acids only. The quantitatively dominating amino acid was proline with a maximum of 976.09 ± 30.52 ng · µl^{-1} (mean ± SD) during the first interval (83% of all identified amino acids) but its content decreased later on. Similar to the temporal variation of sugar concentration (Figure 10), the total content of known amino acids was highest at the beginning, halved during the later intervals but increased at the end of nectar production again (Figure 12). The mean total amino acid concentration (of the identified amino acids only) was 702.82 ± 410.72 ng ·µl^{-1} (mean ± SD), or 0.58, expressed as the coefficient of variation (Vc), i.e., the standard deviation divided by

the mean. The calculated mean correlation coefficient of all 325 possible correlations between the amino acid compositions of the nectar samples was 0.68. The single correlation coefficients ranged from 0.23 to 0.99. Of all correlation, 60.3% were significant on the 0.001 level but 10.1% were not significant at all.

3.4.6 Capitulum visitors

Bats

In total 1,154 bat visits of three phyllostomid species were documented at the three freely hanging capitula. The mean number of visits per capitulum was 384.8 ± 152.6 with a range from 216 to 473 (Table 14). *Phyllostomus discolor* was the most abundant bat with 98.9% of all visits. *Platyrrhinus lineatus* and *Glossophaga soricina* were rare with only 0.7% and 0.4% of all visits, respectively (Table 14).

Table 14 Bat visits to three freely hanging capitula of *P. pendula* between 17:00 h and 03:00 h.

	No. of visits	% of total visits	Visits/capitulum	
			Mean ± SD	Min – Max
P. discolor	1,141	98.9	380.3 ± 146.7	211 - 466
P. lineatus	8	0.7	2.7 ± 3.1	0 - 6
G. soricina	5	0.4	1.7 ± 2.9	0 - 5
Total	1,154	100.0	384.8 ± 152.6	216 - 473

Composition of visitors differed between capitula with different exposition, as seen when comparing a freely hanging capitulum with one next to a horizontally branch. Both capitula (Table 15) flowered during the same night, at the same tree (D181; Appendix 1), and at the same altitude. The horizontally distance between these two capitula was <1 m. Nevertheless, the visiting frequencies differed enormously between these two capitula. The freely hanging capitulum was visited as expected: 97.7% of all 216 bat visits were made by *P. discolor*. *Glossophaga soricina* visited this capitulum five times and no *P. lineatus* individual was observed (Table 15). The most common species visiting the vicinal capitulum next to a horizontally branch was *G. soricina* with 55.4% of all visits. *Phyllostomus discolor* was observed 49 times visiting this capitulum and *P. lineatus* five times (Table 15).

The temporal pattern of bat visits (Figure 13) reflected the temporal pattern of nectar production (Figure 9). First visits were observed between 17:30 h and 17:45 h. The mean visiting frequency between 17:45 h and 24:00 h oscillated with about 13 visits per 15 min with a maximum of 24.6 bat visits between 19:45 h and 20:00 h. The visits decreased rapidly from 24:00 h until 01:30 h. Bats thereafter visited the inflorescences only occasionally (Figure 13).

Table 15 Bat visits to two vicinal but differently exposed capitula of *P. pendula* during the same night of flowering.

		No. of visits	% of total visits
freely hanging capitulum	*P. discolor*	211	97.7
	P. lineatus	0	0
	G. soricina	5	2.3
	Total	216	100.0
capitulum next to a branch	*P. discolor*	49	40.5
	P. lineatus	5	4.1
	G. soricina	67	55.4
	Total	121	100.0

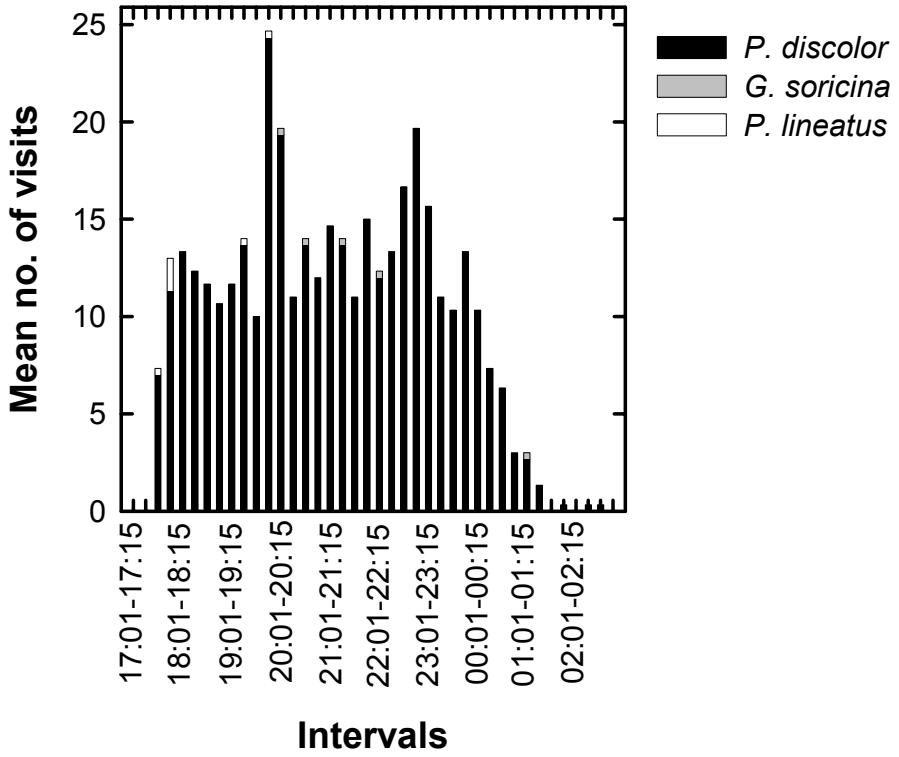

Figure 13 Mean number of bat visits to three capitula of *P. pendula* hanging in clutter-free space in 15-min-intervalls.

Not only the spatial pattern and frequency of visits but also the feeding behavior differed greatly between the three bat species. The most abundant species, *P. discolor*, landed very shortly on a capitulum with the head downwards to reach the nectar, mostly with outstretched wings. The feet were grabbing the upper part of the capitulum and thus got in contact with the sexual organs of the fertile flowers (Figure 14 a). This resulted in the transfer of large quantities of the openly presented polyads onto feet and uropatagium (Appendix 2 b). Sometimes, *P. discolor* used the thumb-claws to grab the capitulum, and accordingly polyads were also found on the wrist around the thumb-claws. *Platyrrhinus lineatus* clung on the lower nectar-secreting

part of the capitulum, grabbing with its thumb-claws and feet the lateral fraction of the fertile part, whereby feet and sometimes the wings got in contact with the fertile flowers (Figure 14 b). *Glossophaga soricina* took nectar on the wing without landing on the capitulum. The long tongue was the only part of the body touching the nectar-secreting and sterile flowers of the capitula (Figure 14 c).

Due to their different feeding behavior, the three bat species differed also in their flight maneuvers. *Phyllostomus discolor* reached the capitulum steeply from below, twisted and landed head downwards on the capitulum. After licking nectar, these bats just let themselves drop of the capitulum backwards, twisted while falling into the right flight-position, and started their next approach. The bats flew between the capitula in a U-shaped curve with the capitula as highest point. The height difference between capitula and turning point was always 2–5 m. Deviating from this behavior they often did not head straight for the next capitulum but flew several wide rounds around the trunk of the tree, a few meters underneath the crown, before accessing the next capitulum. Additionally, *P. discolor* individuals were sometimes observed landing on capitulum buds instead of flowering capitula.

The flight of *P. lineatus* from capitulum to capitulum was similar to that of *P. discolor* but the height difference between capitula and turning point was always <1 m.

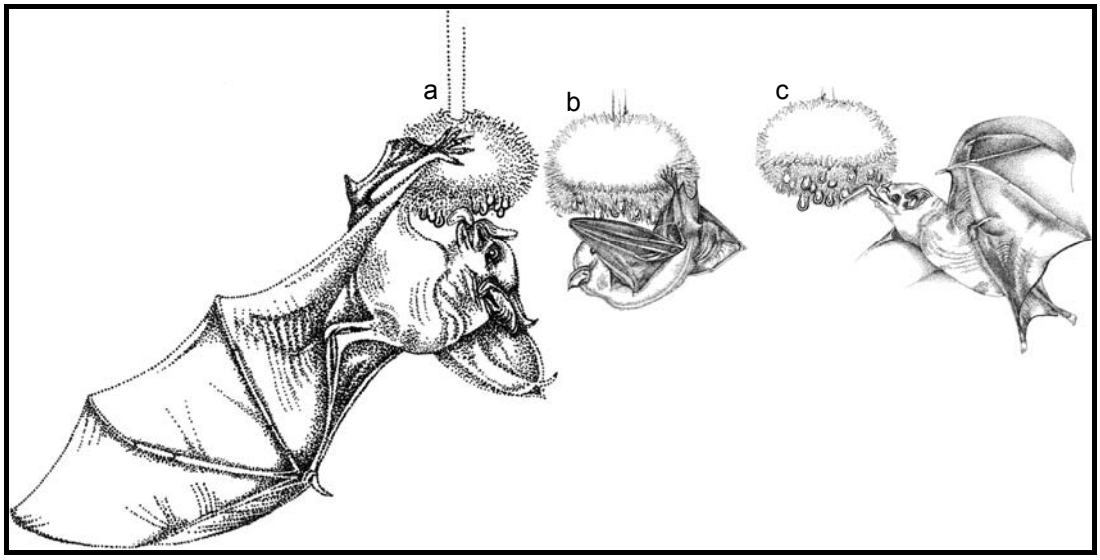

Figure 14 Bats visiting *P. pendula* capitula. a: *Phyllostomus discolor*; b: *Platyrrhinus lineatus*; c: *Glossophaga soricina* (Illustrations by J. Piechowski after photographs; all approx. ⅓ x).

The behavior of *G. soricina* was very different because of a different flight style. Due to their ability to hover in front of the capitula, they did not have to twist their body axis around two times (one time before landing and one after take off). Therefore, the bats moved directly from capitulum to capitulum without the need of falling and ascending to get its own body in the right position. The whole behavior of *G. soricina* was very hummingbird-like due to the direct movement between the

capitula, their nectar licking while hovering, and the common repeated short visits to one single capitulum.

Table 16 Weight and forearm length of bats caught underneath a flowering *P. pendula* crown on October 27, 2004 (17:30 h – 23:00 h).

	n	Male / female	Weight [g]		Forearm length [mm]	
			Mean ± SD	Min – Max	Mean ± SD	Min – Max
P. discolor	23	18 / 5	39 ± 4	28 – 50	59.7 ± 1.4	57.7 – 62.0
P. lineatus	5	4 / 1	17 ± 3	15 – 22	39.6 ± 1.3	38.0 – 41.6

Another clear difference, useful for distinguishing between the three bat species, was their different size (Figure 14). *Phyllostomus discolor* was the largest and heaviest of the three species. *Platyrrhinus lineatus* was clearly smaller and lighter (Table 16). No *G. soricina* individual was captured but the data from Alvarez and co-workers (1991) prove that *G. soricina* is the smallest (forearm length: 31.7 – 38.0 mm; n = 129) and lightest (5 – 17 g; n = 36) of all three species.

Beside these three species, a larger bat species was observed occasionally. Judged from its much larger size than *P. discolor* and the similar foraging behavior, this rare visitor was probably *Phyllostomus hastatus*, the second-largest bat in the Neotropics.

Other vertebrates

Several other vertebrates were observed visiting the capitula of *P. pendula*. Five species from four mammalian orders and one bird were monitored additionally to the bats (Table 17).

Coendou prehensilis was the steadiest visitor besides the bats. Single *C. prehensilis* were found on flowering *P. pendula* trees during nearly every night. In contrast to all other vertebrates, they were feeding on capitulum buds only. They could solely reach capitula close to larger branches by grasping them with their paws while sitting on their hind legs (Figure 16). Just parts of the capitula were ingested by the porcupines. The remaining parts flowered regularly in their normal fashion. Only during one night, two porcupines were observed simultaneously in the same *P. pendula* crown. After feeding on capitulum buds, they rested for several hours on different branches in a tree crown nearby, while emitting gurgling grunts. The slow movements of this medium-sized rodent (weight: 3.60 ± 0.94 kg; n = 70; Richard-Hansen et al. 1999) seemed to be somehow clumsy but because of their 'fifth leg', their prehensile tail, they were able to reach even small branches in the periphery of the crown and to move directly from crown to crown.

Single *Caluromys philander* (Figure 15 c) individuals were seen on most flowering *P. pendula* trees, exploiting nectar all night long. Due to being roughly one

tenth the weight of a porcupine (weight: 0.33 ± 0.06 kg; n = 22; Richard-Hansen et al. 1999), *C. philander* individuals were able to climb down the peduncles, and therefore to reach probably every flowering capitulum.

Table 17 Vertebrates observed visiting *P. pendula* capitula.

Class	Order	Family	Species
Aves	Trochiliformes	Trochilidae	*Amazilia fimbriata* J.F. Gmelin 1788 (Glittering-throated emerald)
Mammalia	Chiroptera	Phyllostomidae	*Phyllostomus discolor* Wagner 1843 (Pale spear-nosed bat)
			Phyllostomus hastatus Pallas 1767 (Greater spear-nosed bat)
			Platyrrhinus lineatus E. Geoffroy 1810 (White-lined broad-nosed bat)
			Glossophaga soricina Pallas 1766 (Pallas' long-tongued bat)
	Primates	Callitrichidae	*Callithrix jacchus* L. 1758 (White-tufted-ear marmoset)
	Rodentia	Erethizontidae	*Coendou prehensilis* L. 1758 (Brazilian porcupine)
	Didelphimorphia	Didelphidae	*Caluromys philander* L. 1758 (Bare-tailed woolly opossum)
	Carnivora	Procyonidae	*Nasua nasua* L. 1766 (Brown-nosed coati)

A *Nasua nasua* (weight: 3.86 ± 0.65 kg; n = 4 males; Gompper and Decker 1998) group was observed during several successive nights in the same *P. pendula* crown (D013; Appendix 1). This group contained four to six individuals including juveniles. Similar to *C. prehensilis* they were feeding on capitula near branches. However, unlike the porcupines, they did not feed on buds but exploited the nectar without destroying the capitula (Figure 15 b). The coati group entered the tree crown shortly after dusk and stayed until midnight. While being in the crown they made a lot of noise. It seemed like there were some struggles between them.

A group of the only primate occurring in the study area, *Callithrix jacchus* (0.33 kg; n = 10 males; Digby in Ferrari 1993), was observed licking *P. pendula* nectar only once. The group consisted of four individuals, which entered the tree on September 25, 2003 at 16:30 h and stayed there for 30 min. They climbed down the peduncles (Figure 15 a), reached the capitula while being suspended by the tail from a branch, or pulled the capitula up with their hands while sitting or being suspended from a branch.

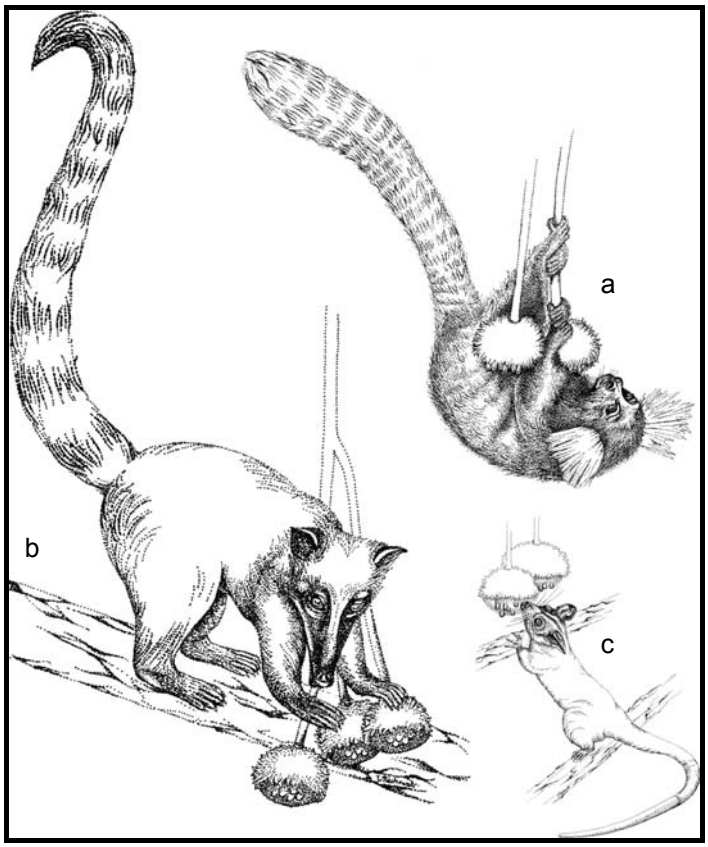

Figure 15 Non-flying mammals visiting flowering *P. pendula* capitula. a: *Callithrix jacchus*; b: *Nasua nasua*; c: *Caluromys philander* (Illustrations by J. Piechowski after photographs; all $^1/_5$ x).

An individual of the hummingbird species *Amazilia fimbriata* was observed visiting capitula only once. It entered the crown approximately half an hour before dusk and stayed there until dusk, visiting numerous capitula. This hummingbird remained several seconds at every capitulum penetrating many nectar-secreting flowers. Before moving to the next capitulum, the bird rested a few times on small branches within the crown.

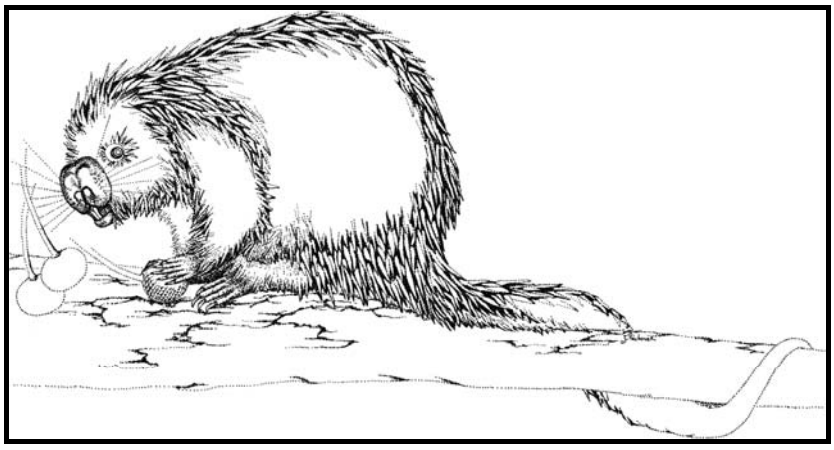

Figure 16 *Coendou prehensilis* feeding on capitulum-buds of *P. pendula* (Illustration by J. Piechowski after a photograph by N.V. Fahlke; $^1/_5$ x).

3.5. Discussion

3.5.1 Phenophases: developmental stages from buds to ripe pods

The data on flowers and capitula of *P. pendula* clearly showed a three times repeated temporally correlated pattern of a) an enormous abortion of reproductive organs followed by a b) very fast development of the remaining ones. First, the total number of initiated inflorescences was reduced during the first weeks. Afterwards, the primary axes of the inflorescences quickly elongated. Second, the number of capitula per inflorescence was reduced by one order of magnitude to the final number of capitula that would actually flower. Growth of peduncle length and diameter of the remaining capitula to maximum size followed rapidly after this reduction. The third phase of abortion and growth occurred during fruit maturation. This last step of reduction by abortion of pods again reached one order of magnitude and happened over a few weeks. The rapid growth to the final size followed shortly thereafter. These highly synchronized events occurred therefore on three morphological levels: first on the inflorescence-level, second on the capitulum-level and third on the pod-level. The reduction on capitulum-level is also described by Hopkins (1986a) but she did not observe the high synchronization within the whole reproduction process: capitulum buds were aborted only in the short time between the growth of the primary axes and peduncle elongation and not during all bud phases. This kind of highly synchronized abortion during the early developmental stages of a reproductive organ is well documented for the fruit abscission in commercial fruit species (see review by Stephenson (1981) and references therein). Reallocation of limited resources is generally suspected to be the proximate reasons for these abortions as resources are usually translocated out of a plant part before abscission and the remaining fruits benefit from these 'surplus resources' (Stephenson 1981). A possible ultimate reason for the overproduction and later abscission might be predator satiation (Janzen 1971), which for *Parkia* was already hypothesized earlier by Hopkins and Hopkins (1983) to be a defense strategy against the high seed-beetle diversity at *Parkia* in the Amazon basin (Hopkins 1983b).

The long inflorescences of *P. pendula* that hang >1 m below the umbrella-shaped crown represent the most extreme case in all Neotropical *Parkia* species (Hopkins 1986a), and clearly match the requirement of well-exposed blossoms for bat-pollination (e.g., Dobat and Peikert-Holle 1985). However, in *P. pendula*, the required robustness of the inflorescences for bat-pollination might not been determined by its pollinators but its dispersers. The largest observed pollinator, the maximal 140 g weighing *P. hastatus* individuals (Kalko and Condon 1998), are much lighter than the presumed disperser, *C. jacchus*, which weighs on average 330 g

(Digby in Ferrari 1993) and climbs down the inflorescence-axes to feed on nectar but mainly later on the seedpod-gum.

3.5.2 Capitulum and flower morphology

The elongated styles of the nectar-secreting flowers are typical for the three species of section *Platyparkia* (Luckow and Hopkins 1995). They are not exserted beyond the tube of the flower during flowering in the nectar-secreting flowers of section *Parkia* (Luckow and Hopkins 1995), if ever present (Hopkins 1986a). The convergent nectar-secreting flower types of both sections can be understood as modifications from fertile, hermaphroditic flowers, since the common ancestor of both sections had fertile flowers only, as seen in the basal, paraphyletic section '*Sphaeroparkia*' (Hopkins 1998). This morphological difference between the two sections can be explained by their differences in the capitulum structure. The capitula of section *Parkia* are biglobose with the nectar-secreting flowers forming a groove between the fertile and staminodial flowers (Hopkins 1986a). All secreted nectar is collected in this groove and thereby kept from dropping to the ground. Such a groove is lacking in the oblate capitula of section *Platyparkia*, where the nectar-secreting flowers are at the flattened apex, i.e., at the bottom of the hanging capitula. The nectar-keeping task is performed in these species by the elongated styles. Large nectar drops are taken up by the styles adhesively and thereby kept away from dropping. Such floral devices are often found in bat-pollinated flowers with large amounts of nectar and downwards oriented flower openings (von Helversen 1993).

Hopkins (1986a) reports that the anthers of nectar-secreting flowers often dehisce and probably release their polyads into the nectar. This was never observed in *P. pendula*. Even air-dried nectar-secreting flowers had only slightly opened anthers. However, nectar that is secreted at the flower base could get in contact with the polyads while running out of the flower leading to a leaching of amino acids into the nectar. This could be the reason for the relatively high and stable content of proline in *P. pendula* nectar; pollen-contaminated nectar is known to have increased amino acid contents, especially with respect to proline (Gottsberger et al. 1984, 1990).

The lack of correlation between the number of flowers and capitulum size in *Parkia* could be a hint for an 'optimal size' of *Parkia* capitula of 5-8 cm in length regardless of the number of flowers. Only the very large capitula of *P. gigantocarpa* and the small capitula of *P. pendula* do not fit in this picture.

3.5.3 Breeding system

The bagging-experiments showed self-incompatibility of *P. pendula* and therefore its xenogamy. Furthermore, the large diameter of the capitula and the protandry

resulted in an outcrossing index (OCI) of 4. This OCI-value characterizes species that are adapted for outcrossing (Cruden 1977). Nevertheless, evidence for selfing in *Parkia* was found by Hopkins (1984) in isolated *P. discolor* and *P. ulei* trees at the Museu Paraense Emílio Goeldi site in Belém.

The P/O ratios of most xenogamous, animal-pollinated plants are between 1,200 : 1 and 8,000 : 1 and therefore significantly higher than facultative xenogamous and autogamous species (Cruden 2000). The P/O of *P. pendula* with 397.3 ± 60.2 : 1 was clearly below the lower limit of xenogamous plants, which confirms the general trend of plants with polyads or pollinia of having lower P/O ratios than those with monads (Cruden 2000). This is especially known for the species of the Mimosaceae genera *Calliandra* with a P/O between 246.1 ± 24.5 and 863.3 ± 42.3 (Cruden 1977), and *Inga* with a P/O between 310.9 and 1,178.2 (Koptur 1994). Additionally, these species have ratios of pollen grains in a polyad per ovules and carpel between 0.79 and 1.74 (Cruden 1977, Koptur 1994), comparable with the 1.19 in *P. pendula* (32 pollen grains per polyad and 27.1 ovules). Such a more or less equal number of pollen grains per polyad and ovula per ovary can lead to single-paternal seeds per fruit. Successful fertilization of all ovula of a single fertile flower can therefore be obtained by a single polyad deposited at the stigma. This case is probably rather common in *P. pendula* despite the fact of high pollen loading of the bat's feet and uropatagium arising from the high number of polyads per capitulum and the high visitation-rate. Three facts lead to this consideration. Firstly, it is known, that large pollen quantities get lost on the body of the bats due to intense grooming between flower-visiting (von Helversen 1993, Tschapka and Dressler 2002). These polyads are lost for pollination. This behavior of the visiting bats is probably the reason for pollen-findings by de Carvalho (1961) and Hopkins (1984) in stomachs of bats shot underneath flowering *P. pendula* trees. Secondly, the bat's surface, which is dusted with pollen (feet and uropatagium), is very large in comparison with the tiny surface of the stigma, which limits the polyad deposition on the stigmas during these very short visits. Thirdly, the number of flowers left at the capitula, after all unfertilized flowers were aborted and before pod development, was relatively low, with around 50–100 flowers, which is a fertilization rate of only 6–12%.

3.5.4 Odor

Odor of buds and flowers may have different functions: bud odor often has to prevent the bud from being infected by herbivores (mainly by insects) or to attract specific herbivore-predators after infection (Pichersky and Gershenzon 2002). Flower scent is emitted to attract olfactory-orienting pollinators (Knudsen et al. 1993, Piechulla and Pott 2003). The different odor composition in buds and flowering capitula of *P. pendula* hints towards such different functions of scent.

The main components of bud scent, α-pinene and geranyl acetone, are known plant-produced toxins (Redak and Cates 1984). Furthermore, α-pinene is not only known to be toxic for many insects (Redak and Cates 1984) but also for mammals (Falk et al. 1990). The fact, that one capitulum bud emitted four additional odor compounds beside the two main compounds might be a change in scent composition induced by herbivores. Own observations show that buds are very vulnerable to insects depositing their eggs inside, probably bruchids, that are known to parasite on *P. pendula* seeds (Hopkins 1983b).

The floral odor of *P. pendula* was found to be that of over-ripe fruits, not usually unpleasant in small quantities but heavy and sickly when concentrated (Hopkins 1984). Eighty to over 95% of *P. pendula* floral scent components are monoterpenes, all very common in floral scents (Knudsen et al. 2006, Knudsen et al. 1993) and known to have a wide smell spectrum from spicy and resin-like to sweet and citrus-like (Knudsen et al. 1993). This kind of fragrance is not very common in bat-pollinated plants (Dobat and Peikert-Holle 1985). Generally, bat-pollinated plants are reported to be strongly fetid and pungent (Pettersson et al. 2004) or, mainly due to sulphur components (Kaiser and Tollsten 1995), sulphury-onion- or mushroom-like (Knudsen and Tollsten 1995). These compounds are only very rarely present in flower bouquets (Knudsen et al. 1993) but were found in 17 out of 26 analyzed bat-pollinated plant species from the New World (including the present work), in 5 out of 8 analyzed African species and in one Asian species (Azuma et al. 2002, Bestmann et al. 1997, Kaiser and Tollsten 1995, Knudsen 1999, Knudsen and Tollsten 1995, Pettersson et al. 2004, Pettersson and Knudsen 2001, Varassin et al. 2001, Winkler 1998). These analyses show clearly, that sulphur-containing fragrances are common in bat-pollinated flowers, especially in the New World, where they are found regularly in much higher quantities than in the Paleotropics. They are even suspected to be key substances in the co-evolution of bats and bat flowers (Kaiser and Tollsten 1995). On the other side, it is also obvious from the analyzed 26 Neotropical plants and supported by the fruity non-pungent odor of *P. pendula*, that not even in the Neotropics all bat-pollinated flowers have sulphur compounds or other combinations of scent compounds that are similar to the sulphur smell as suspected by von Helversen et al. (2000). This lack in sulphur compounds in *P. pendula* floral scent could be due to phylogenetic constraints. However, Pettersson et al. (2004) found traces of the scentless dimethyl sulfoxide in the odor of the African *P. bicolor*, and Morris et al. (1978) detected three to seven sulphur amino acids in the seeds of 15 analyzed *Parkia* species including *P. pendula*. This indicates that the physiological capability to synthesize sulphur compounds occurs in this genus and even in *P. pendula*. Pettersson et al. (2004) explain the low number of African bat-pollinated species having significant amounts of sulphur components (only

Adansonia digitata; Pettersson et al. 2004) with the observation that the large African pteropodid bats feed mainly on flowers elevated from the canopy whereas the small American glossophagine bats forage in more cluttered vegetation. In such a cluttered vegetation specific and unusual odor compounds may reduce foraging time and energetic costs (Pettersson et al. 2004). Such a specific olfactory guide might not be necessary in the case of *P. pendula* where the capitula are hanging freely on long peduncles underneath the umbrella-shaped crown.

The sulphur-containing scent is an important long-distance attractant (Dobat and Peikert-Holle 1985, von Helversen 1993) but also permits the precise, short distance localization of single flowers (von Helversen et al. 2000). Precise localization of the capitula of *Parkia* may be achieved by bats in a combination of visual and acoustical cues. Red (dark for bats with retinas dominated by rods; Suthers 1970, Winter et al. 2003) capitula are distanced from the foliage and well visible against the brighter sky (like in *P. pendula*), whereas the capitula of species with yellow (bright) capitula flower in general more closely to the dark foliage (e.g., *P. gigantocarpa*) and increase their visibility in this way as well (Hopkins 1984). Additionally, the flagelliflory itself is probably an adaptation to localization by bats. These freely hanging capitula might be an easy target for echolocating bats as it was shown for the flagellichorous *Gurania spinulosa* and its dispersal agent *P. hastatus* (Kalko and Condon 1998). In the case of the relatively odorless *G. spinulosa*, the flagellichorously offered fruit is an important cue for the bat to find the fruit (Kalko and Condon 1998) in contrast to many other bat-dispersed plants like figs, where odor is a main cue (Kalko et al. 1996).

Pettersson et al. (2004) assumed, that the higher sulphur amounts in the scent of American bat-pollinated plants might be a result of co-evolution with glossophagine bats which are foraging in less open vegetation than African bats. This assumption implies a possible olfactory distinction between flowers visited by glossophagine bats and flowers, which are visited by the group of larger, less specialized bats. This idea cannot be confirmed after comparing all available data. Some species, which are only visited by glossophagine bats like *Passiflora galbana* (Varassin et al. 2001) and *Weberocereus tunilla* (Tschapka et al. 1999) do not contain any sulphur components. On the other hand, plants like *Ochroma pyramidale* and *Ceiba pentandra*, both heavily visited by large bats (Gribel et al. 1999, Tschapka and Dressler 2002) do contain large amounts of sulphur components in their odor.

Sulphur-containing odors should therefore be seen like most other pollination syndrome characteristics: a plant species obviously does not have to show all syndrome characteristics to gurantee pollination by bats (Dobat and Peikert-Holle 1985). This is especially true if functions associated with a special characteristic are realized by other features such as the short distance localization of

P. pendula capitula, which probably is achieved by the bat's echolocating and visual senses, guided by contrasty and isolated blossoms rather than olfactory.

Several publications report that a change in floral scent production after maximum scent emission (Effmert et al. 2005) or after pollination (Schiestl and Ayasse 2001) maximizes the reproductive success of the plants, due to a pollinator guidance to unpollinated flowers (Schiestl and Ayasse 2001) or due to a herbivore-repelling effect (Effmert et al. 2005). Since such interactions have not been observed in *P. pendula* and the detected components have no known influence on herbivores, the change in odor composition is interpreted as the consequence of the beginning wilting of the flowers. Often, decreasing scent emissions were observed with flower aging (Dötterl et al. 2005, Effmert et al. 2005, Muhlemann et al. 2006, Theis and Raguso 2005), which is understood as an adaptation to the high energy costs connected with scent production and maintenance by the flowers (Dudareva et al. 2000). The different speed of this decline between the scent compounds may be due to differences in biosynthetic pathways (Dudareva et al. 2000, Theis and Raguso 2005). An earlier decline and fading of some components (e.g., neral) in *P. pendula* therefore led to a reduction of compounds during the last observation interval and a relative increase in compounds still present, like *trans*-β- ocimene.

3.5.5 Nectar

Nectar quantity

The median total nectar volume per capitulum of *P. pendula* is more or less equal to the mean nectar volume of *P. bicolor* (8.7 ± 2.3 ml; Grünmeier 1992) and *P. gigantocarpa* (5–7 ml; de Carvalho 1960). Differing nectar volumes are known for *P. biglobosa*. Pettet (1977) measured a volume of 9–10 ml in Nigeria, whereas Pettersson and Knudsen (2001) reported only 2.4 ± 2.1 ml from individuals in Senegal, while Baker and Harris (1957) removed up to 5 ml per capitulum from individuals in Ghana. Additionally, measured nectar quantities of single harvested capitula of *P. igneiflora* (Hopkins 1984) and observations of large drops of nectar in *P. discolor* (Vogel 1968), *P. speciosa* (van der Pijl 1936) and *P. filicoidea* (Hopkins 1983a) prove that large nectar quantities are common for bat-pollinated *Parkia* species, whereas melittophilous *Parkia* species are lacking nectar (Hopkins et al. 2000). No significant correlations could be found between the total nectar volume and number of nectar-secreting or total flowers of these few studied *Parkia* species. One reason might be the enormous variation between geographically distinct populations of the same species (e.g., *P. biglobosa*) already mentioned for *P. bicolor* by Hopkins (1983a) and Grünmeier (1990). Another reason could be found in the co-evolution between *Parkia* and bat species. There should be a selection pressure on the plant towards a

lower nectar secretion because of a) lower energetic costs, but more chiefly because b) smaller nectar amounts force pollinators to increase their visitation rate for obtaining an equal amount of nectar, which raises the plant's probability for being sufficiently cross-pollinated (Gould 1978, Heithaus 1982, von Helversen and Winter 2003). On the other hand, these nectar quantities must be still large enough to attract the pollinating bats (Dobat and Peikert-Holle 1985, Heithaus 1982, von Helversen and Winter 2003, Zimmerman 1988). The result of these pressures seems to be a nectar volume of (2) 5–8 (10) ml per *Parkia* capitulum independently of the number of flowers per capitulum.

Apparently, there are three different temporal traits of nectar production in bat-pollinated flowers. Some species start production around dusk with increasing rates until midnight and a decrease thereafter until the end of production early in the morning (von Helversen and Voigt 2002, Nassar et al. 1997, Tschapka et al. 1999). A second group of plants produces its nectar exclusively before flower opening as, e.g., *Passiflora mucronata* (Varassin et al. 2001) or *Phenakospermum guyannense* (Kress and Stone 1993). The third group has a high nectar production at the beginning of anthesis around dusk followed by few hours of more or less stable production on a lower level and a rapid decline afterwards. This last temporal pattern is typical for *P. pendula* and its two African congeners *P. bicolor* (Grünmeier 1990) and *P. biglobosa* (Pettersson and Knudsen 2001) as well as, e.g., *Ceiba pentandra* (Elmqvist et al. 1992, Gribel et al. 1999, Singaravelan and Marimuthu 2004). There are further distinctions between the first and third group beside this difference in nectar production, although both groups are clearly adapted to pollination by bats. The first group members (*Helicteres baruensis*, *Pilosocereus moritzianus*, *Stenocereus griseus*, *Subpilocereus horrispinus*, *S. repandus*, and *Weberocereus tunilla*) show clear adaptations to glossophagine bats like relatively small amounts of nectar (< 1–2 ml) and the necessity for bats to hover in front of the flower to reach the nectar, excluding thereby visits by larger bats. Consistently, these species are visited by glossophagine bats only (von Helversen and Voigt 2002, Nassar et al. 1997, Tschapka et al. 1999). On the other side, the third group produces much more nectar per blossom. The blossoms are less fragile and provide landing-space and are therefore pollinated by 'big bats' (von Helversen 1993). These are mainly *Phyllostomus discolor* and *P. hastatus* in the New World (Gribel et al. 1999; 3.4.6.) and large pteropodid bats like *Pteropus tonganus* (Elmqvist et al. 1992), *P. giganteus* (Singaravelan and Marimuthu 2004), *Megaloglossus woermanni* (Grünmeier 1990), *Epomophorus gambianus*, *Eidolon helvum*, and the smaller but similar foraging *Nanonycteris veldkampii* (Baker and Harris 1957) in the Old World. The temporal differences in nectar production might therefore be a further distinction between glossophagine flowers and flowers pollinated by larger bats.

Nectar quality

Sugars

Nectar sugar concentration of 15.9 ± 4.4% (w/w) and its hexose-dominated composition are typical for bat-pollinated flowers (Baker and Baker 1990, von Helversen 1993, Paula et al. 1997, Schwerdtfeger 1996). Changes in nectar sugar concentration during anthesis with highest values during highest nectar production are also often reported (von Helversen and Voigt 2002, Nassar et al. 1997, Singaravelan and Marimuthu 2004). However, a change in sugar composition during anthesis with a change in nectar category was discovered only recently in two varieties of *Carum carvi* (caraway), a protandrous species with flowers lasting up to 15 days (Langenberger and Davis 2002). The sugar ratio was 0.133 and 0.182 during the male phase and 0.025 and 0.038 in the female phase for the two varieties, respectively. This difference was driven by a drastic decline in sucrose concentration whereas the glucose and fructose concentration stayed more or less stable (Langenberger and Davis 2002). Therefore, the initial as well as the final sugar ratio and its change are similar in *C. carvi* and *P. pendula*. The time between the changes in sugar quality is the only difference between the two species: several days in *C. carvi* (Langenberger and Davis 2002) versus several hours in *P. pendula*. Langenberger and Davis (2002) speculated about the physiological reasons for this change and preferred pre-secretory differences like different supplies of carbohydrates entering the nectaries or even variable routes for pre-nectar movement and escape. Another possibility is an invertase-induced post-secretory sucrose cleaving into fructose and glucose as found in extrafloral nectaries of myrmecophytes of the genus *Acacia* (Heil et al. 2005) and probably also in floral nectar of *Capparis spinosa* (caperbush) (Petanidou et al. 1996). But this explanatory approach implies a temporal variation in invertase activity. Additionally, all nectar was removed from the capitula after every sampling, so that only freshly produced nectar was sampled. Doubtlessly, there is more research needed to explain these temporal changes. Nevertheless, these new findings demonstrate clearly that there is a high variability in floral nectar sugar composition not only between flowers, individual plants, and populations (Galetto and Bernardello 2004, Herrera et al. 2006, Lanza et al. 1995, Schmidt 1998, Schwerdtfeger 1996) but also between different phases of anthesis.

The energy density of *P. pendula* is similar to the group of high nectar density plants defined by Tschapka (2004). These plants, like *Vriesea gladioliflora*, *Mucuna holtonii*, and *Ochroma pyramidale*, offer an energy density of several thousand $kJ \cdot ha^{-1} \cdot d^{-1}$ but flower a short time per year only (Tschapka 2004). This high energy density may be reached in two different ways, either by a high density of individuals

with a low number of flowers and nectar (*V. gladioliflora*, *M. holtonii*) or by a low number of trees with a high number of flowers and a profuse nectar production (*O. pyramidale*) (Tschapka 2004). *Parkia pendula* corresponds to the latter pattern, being therefore a typical representative of the cornucopia flowering pattern (*sensu* Gentry 1974). Such a high energy density, achieved by few large trees of the cornucopia flowering pattern (i.e., the nectar resource is patchy distributed in space and time), seems to be typical for trees that are pollinated by large bats, since this pattern is also found in *C. pentandra* (Gribel et al. 1999).

Although the calculated nectar and sugar quantities are relatively high, they are still far below the calculated 200 l of nectar in a flowering period of five weeks, produced by a relatively young *C. pentandra* tree in Amazonia (Gribel et al. 1999).

Amino acids

The total number of 21 different amino acids found in *P. pendula* nectar corresponds very well with nectar analyses of other taxa (Gardener and Gillman 2001, Gottsberger et al. 1989a, Koptur 1994, Petanidou et al. 1996). Unfortunately, only eleven of them could be identified although 16 of the 20 protein-building amino acids were used as external standards. Therefore, a minimum of six (if the four 'normal' amino acids that were not included in the external standard were within the unidentified) and a maximum of ten (if all unidentified amino acids were non-protein amino acids) non-protein amino acids can be assumed to occur in *P. pendula* nectar what is comparable with earlier works (Gardener and Gillman 2001, Gottsberger et al. 1989b, Koptur 1994, Petanidou et al. 1996).

The mean concentration of the identified amino acids was quite high compared with previously published results (Gardener and Gillman 2001, Gottsberger et al. 1984, 1989b, 1990, Petanidou et al. 1996). Additionally, the composition of the identified amino acids is clearly dominated in all samples by the protein-building amino acid proline. This could be a clue for a contamination with pollen, since proline is known to be one of the main amino acids of pollen and to dilute easily and in large amounts into the nectar if pollen is inserted (Gottsberger et al. 1984, 1990). Since in *P. pendula* capitula the polyad-presenting anthers of the fertile flowers are spatially separated from the nectar-secreting flowers and sampling was conducted very carefully in order to avoid contamination, pollen from the fertile flowers cannot be the source of proline. Even if never exserting the corolla, the anthers of the nectar-secreting flowers contain polyads. It is reported that these anthers dehisce regularly like the anthers of the fertile flowers (Hopkins 1986a). Although, this was never observed during this study the polyads of the nectar-secreting flowers are the most reasonable source for the high proline content, as nectar is produced at the flower base and could easily get in contact with the polyads

while passing the anthers. The high proline content could enhance the pollination success, should bats be able to prefer proline-rich nectar and even get a benefit from it, as recently shown for proline-rich nectar preferred by *Apis mellifera* (Carter et al. 2006). Future studies should investigate by feeding-experiments, whether there is any evidence for an evolutionary significance for this observation in the *Parkia*-system.

Gardener and Gillman (2001) used the coefficient of variation (Vc) as an index for the variability in total amino acid concentration among samples. After examining 30 plant species the authors got an average Vc of 0.67 per species (Gardener and Gillman 2001) which is slightly higher than the Vc of 0.58, calculated for the identified amino acid concentration in all 26 samples of *P. pendula*. It expresses a high variability in amino acid concentration between the nectar samples of a species. A reason for the slightly lower Vc could be the nocturnal anthesis of *P. pendula*, since day-to-day environmental variations like temperature and sunlight are proposed to be the main source of variability (Gardener and Gillman 2001) and these factors do not vary greatly during night.

The correlations between amino acid compositions of the single nectar samples differ much wider from the results of Gardener and Gillman (2001). They found all their 544 computed correlations to be statistically significant on the 0.001 level and their average correlation coefficient of all 30 observed species was 0.88. These high correlations led the authors to assume species-specific amino acid compositions fixed by genetic processes (Gardener and Gillman 2001). On the first view, this is somehow contradicted by the current results of only 60.3% of all 325 correlations being significant on the 0.001 level and 10.1% being not even significant at all. However, Gardener and Gillman (2001) included only samples of similar aged flowers in their analyses to avoid possible differences due to flower age as shown previously for two shrub species (Gottsberger et al. 1990, Petanidou et al. 1996). The sampling protocol of the present work was designed to represent the total flower anthesis. The greater differences within the samples in amino acid composition compared with Gardener and Gillman's (2001) results may therefore be interpreted in accordance with Gottsberger et al. (1990) as a product of flower aging. Unfortunately, this could only been shown graphically and not statistically (as e.g., in odor composition) due to the loss of 58% of all nectar samples during transportation.

3.5.6 Capitulum visitors

Bats

Quantitative data of bat visits per blossom of trees are very difficult to obtain due to the height of the trees and the unfavorably light situation (Gribel et al. 1999, Vogel 1968). The only given information about the number of pollinators of *P. pendula* is by Hopkins (1984). She once saw a large flock of several hundred bats within a *P. pendula* crown (Hopkins 1984). The recent results are similar to her observation. Flowering *P. pendula* trees, with up to 473 bat visits per capitulum and night, are a highly attractive resource for bats. Such large numbers of bat visits are known for a few other Neotropical trees like *Ceiba pentandra* (Gribel et al. 1999, Heithaus et al. 1975) *Ochroma pyramidale* (Heithaus et al. 1975) or *Parkia decussata* (Hopkins 1984), all of which being pollinated by large, unspecialized bats, mainly of the genus *Phyllostomus*. That all these species are pollinated by unspecialized bats, prove the similarities in temporal nectar production, nectar quantity, and energy density of these trees to be related with pollination by large bats. Another common detail of the pollination of this group of trees is the group-foraging of their large pollinators (de Carvalho 1960, Heithaus et al. 1975, Hopkins 1984, Sazima and Sazima 1977, Vogel 1968). This feeding strategy seems to be stimulated by large nectar sources (Sazima and Sazima 1977) and may maximize the foraging efficiency since these resources are mostly patchy distributed in space and time (Heithaus et al. 1975, Wenrick Boughman 2006).

A preference of well exposed blossoms over blossoms in cluttered space was also observed by Heithaus et al. (1974) and Vogel (1968) for *P. discolor*. The few visits of *P. discolor* to the less exposed capitulum of *P. pendula* are furthermore interpreted as the result of learning of only a few (one?) bats, since 70% of all these visits are executed between one hour only and many unsuccessful visiting attempts were observed shortly before. The less exposed capitula are on the other hand the preferred places of the smaller bats, especially *G. soricina*, as previously observed by Heithaus et al. (1974) at *Bauhinia pauleta*. These different feeding preferences may have two reasons. Firstly, the competition for nectar is lower for the smaller bats at capitula in cluttered space since these blossoms are less frequented by the larger bats. Secondly, the behavior of the small bats might also be a predator avoidance strategy. The rare visitor *Phyllostomus hastatus* (weight: 92-140 g; Kalko and Condon 1998), which was seen on freely hanging capitula only, is known to feed on small bats (Santos et al. 2003). A similar behavior was observed for *Glossophaga commissarisi* and *Lichonycteris obscura*, who avoided free-standing flowers during bright nights at La Selva, Costa Rica, probably to avoid predation by small owls (von Helversen 1993).

Nevertheless, these observations of preferences of the different bat species for freely hanging or obscured capitula have to be confirmed by experiments with bats in screen tents as performed by Kalko and Condon (1998).

Both small bats, *G. soricina* and *P. lineatus*, were never reported before to visit flowering *P. pendula* (de Carvalho 1961, Hopkins 1984, Rodriguez-H. and Hopkins 2000) although both species are known to feed on nectar (e.g., de Carvalho 1960, Heithaus et al. 1975, Sazima et al. 1999, Vogel 1968). In addition, it is the first observation of a specialized nectar-bat visiting a *P. pendula* capitulum (Rodriguez-H. and Hopkins 2000), but they are known previously to visit other *Parkia* species (Hopkins 1984). Together with the two new species, eleven bat species out of four phyllostomid-subfamilies (Phyllostominae, Stenodermatinae, Carolliinae and Glossophaginae) are known now to feed on *P. pendula* (de Carvalho 1961, Hopkins 1984, Rodriguez-H. and Hopkins 2000).

Because *G. soricina* did not get in contact with the fertile flowers due to its hovering flight, this species is categorized as 'nectar-thief', i.e., it got nectar without pollinating because of a mismatch of morphologies (or here: behavior as a consequence of morphology) (Inouye 1980). Highly specialized flower bats are also reported to be nectar-thieves in *Ochroma pyramidale* (Tschapka 2003), *Mabea fistulifera* (Vieira and Carvalho-Okano 1996), and *Marcgravia nepenthoides* (Tschapka and von Helversen 1999). It is either an energetically reasonable strategy for glossophagines to leave their unrivaled flowers and compete with larger bats for the large quantities of nectar, or a behavioral flexibility as consequence of feeding on a highly ephemeral resource (Tschapka 2003).

These data show that *P. discolor* is the main pollinator of *P. pendula* and confirm reports by de Carvalho (1960, 1961) and Hopkins (1984). *Phyllostomus hastatus* is probably a similarly efficient pollinator; however, it is comparably rare in the study area. The small bat *P. lineatus* is most likely a less efficient pollen vector because due to its visiting behavior it gets only slightly in contact with the fertile flowers. Therefore, *P. pendula* depends on pollination by large, unspecialized bats, which is interpreted as 'conservative' in bat pollinated plants (von Helversen 1993).

The capitula that are hanging far below the broad and flattened crown enable the best accessibility for the large and – in comparison to glossophagine bats – relatively bad maneuvering large bats. However, the capitula would hang in the understory vegetation, and not in clutter-free space, if the understory trees grow into or close to the *P. pendula* crowns, which is an otherwise common feature of the vegetation structure of the studied forest. This would result in a rather incomplete pollination of the self-incompatible *P. pendula*. Measurements showed that there is indeed always a free uncluttered airspace of about 5 m underneath a *P. pendula* crown, suggesting that the growth of understory trees is somehow inhibited by *P.*

pendula. Moreover, lianas were very seldom seen in *P. pendula* crowns but were common in nearly all tree crowns nearby. Recently, some chemical compounds from *P. pendula* leaves with allelopathic activities were identified in laboratory experiments (Souza Filho et al. 2005). Further research is now needed, to show the relevance of these allelopathic substances under field conditions.

Other vertebrates

It is known that the large nectar quantities of bat pollinated plants – especially those pollinated by large bats – attract a wide range of nocturnal non-flying mammals (Tschapka and Dressler 2002). This holds especially true for the genus *Parkia* in the Old World as well as in the New World. An African dormice (*Graphiurus* sp.) and two prosimians (*Perodicticus potto* and *Galago* sp.) were observed nectar-feeding on *P. bicolor* (Grünmeier 1990, P. Agland in Hopkins 1983a), black lemurs (*Eulemur macaco*) on *P. madagascariensis* (Birkinshaw and Colquhoun 1998), unidentified squirrels on *P. filicoidea* (J.D. Chapman in Hopkins 1983a) and most probably a kinkajou (*Potos flavus*), a large possum (cf. *Didelphis* sp.), and two more unidentified non-volant mammals were observed on *P. pendula* (Hopkins 1981). All of these – as well as the two nocturnally nectar-feeding mammals *C. philander* and *N. nasua* observed in the present study – could theoretically act as pollinators but they are unlikely to be important if pollinating at all. The small mammals *C. philander* and *Graphiurus* sp. were never observed leaving the tree crown they were feeding in. Additionally, their nocturnal movement range is probably too small to reach another flowering *Parkia* tree on a more regular basis. Thus, they are only transferring pollen within one tree which probably does not lead to a successful pollination since these species are unlikely to be geitonogamous (Grünmeier 1990, Hopkins 1983a). The larger mammals might probably have a range wide enough to move between *Parkia* trees within one night, however, they were all not common enough to play an important role in the pollination of the corresponding trees (Grünmeier 1990, Hopkins 1984).

The change to nocturnally feeding of predominantly diurnal animals like *N. nasua* (Gompper and Decker 1998) and *E. macaco* (Birkinshaw and Colquhoun 1998) indicates the enormous importance of these nectar sources for these mammals. Additionally, the flowering and fruiting time in *P. pendula* coincides with the dry season in the study area, which is known to be a period of scarcity of ripe fruits in tropical wet forests (e.g., Peres 1994, van Schaik et al. 1993). Dietary switching appears to be the most important behavior of frugivorous mammals to mitigate the impact of scarcity (van Schaik et al. 1993). Nectar (Ferrari and Strier 1992, Peres 1994) as well as *Parkia*'s seedpod gums (Peres 1994, 1996, 2000) are known to be important nutritional sources for mammals, mainly primates, during the dry season.

Peres (2000) analyzed the concept of keystone plant resources in detail, using the possible keystone resources of seedpod gums of *P. nitida* and *P. pendula* as an example. He used the temporal redundancy of the resources, their degree of consumer specificity, reliability, and abundance as variables for a formal definition of keystone resources. Both species failed this definition mostly due to a high consumer specificity (only primates and parrots fed on the gum) and a low abundance in the studied central-western Brazilian Amazon (21 fruiting *P. pendula*/200 ha) (Peres 2000).

If this keystone plant resource concept is applied to the results of the present study with a wider resource definition – including all reproductive organs of *P. pendula* from capitulum buds to ripe pods – *P. pendula* would pass the definition as a keystone plant resource for mammals of the studied fragment of Atlantic Forest. The consideration of all reproductive organs leads to a broader consumer-spectrum and therefore a lower consumer specificity of the resource. Additionally, the density of adult trees is 10-20 times higher than in the Amazon forest studied by Peres (2000). On the other side, the resource reliability was quite low in the second (very wet) year of this study and the nutritional importance of *P. pendula*'s reproductive organs for the single mammalian species is still unknown. Therefore, more research is needed before labeling *P. pendula* as a keystone plant for the mammal fauna of the northern Atlantic Forest fragments, indicating its significance for the conservation of the local mammal fauna.

4. Population Phenology and Seed Production of *Parkia pendula* – Forest Edge Zone *vs.* Interior

4.1. Abstract

Edge effects with respect to the phenology of trees are reported in literature for newly created edges only. Results of a two-year lasting phenological study of *P. pendula* are presented, in which the edge zone and the forest interior of an old Atlantic Forest fragment in Pernambuco, Brazil, were compared. Begin of defoliation, maximum defoliation, and the time of newly foliated crowns was significantly later in the forest edge zone than in the forest interior during the first year of observation. On the other hand, no difference could be observed for the time of flowering and fruiting between habitats and years. Most trees of the edge zone and forest interior flowered highly synchronously during the first year but only three edge trees flowered during the second year. Furthermore, defoliation was significantly earlier during the second year. These differences between the two years of observation are explained with enormous differences in precipitation: the pre-flowering phase during the second year had nearly two times the normal precipitation, which probably resulted in a reduced flowering. The second year's earlier leaf fall was probably caused by its prolonged dry season. It is very likely that the heavy irrigation of adjacent sugarcane fields caused the delayed begin of the water stress-induced defoliation of forest edge trees during the first year. The calculated seed production per tree was more than 12 times higher in the edge zone than in the interior because of a significantly higher number of capitula per tree. This too might be a result of an influx of nutrients and water from the sugarcane fields into the edge zone. Long-term observations are needed to verify the here proclaimed high sensibility of phenological events of *P. pendula* to climatic variability.

4.2. Introduction

Plant phenology, i.e., the temporal patterns of flowering, fruiting, and leafing determines largely the interspecific relationships in ecosystems and therefore ecosystem functioning. All animal species depend on the carbon-fixing plants as the basis of every food-web directly, such as folivorous, nectarivorous, and frugivorous species, or indirectly, as predators of primary consumers (Heideman 1989, Newstrom et al. 1994). On the other hand, most plant species in the tropics depend on services provided by animals, like pollination and seed dispersal (Bawa 1990, Garber and Lambert 1998). Knowledge of timing, duration, and intensity of plant phenology is therefore essential for the understanding of the ecology and evolution of species and their inter- and intraspecific relationships (Bullock and Solís-Magallanes 1990, Frankie et al. 1974). This is demanded for all levels of plant

phenology from sub-individual levels (e.g., for single flowers or branches) up to guild- and community levels (Frankie et al. 1974, Newstrom et al. 1994).

Tropical rainforests harbor the greatest diversity of phenological patterns since they lack a winter season, which in temperate zones synchronizes the phenology of most plant species into annual cycles at all phenological levels (Newstrom et al. 1994). This results – together with the high plant and animal diversity – in a much higher complexity than in temperate zones (Bullock and Solís-Magallanes 1990), where most studies concerning plant phenology were performed (Frankie et al. 1974, Newstrom et al. 1994, Reich 1995).

There is evidence, that climatic events often trigger plant phenology even in tropical regions with their limited interannual variation of e.g., irradiance and precipitation (Anderson et al. 2005, van Schaik et al. 1993, Zimmerman et al. 2007). The phenological processes are therefore very sensitive to climatic variability between years, wherefore long-term surveys are indispensable to detect sound patterns (Frankie et al. 1974, Newstrom et al. 1994). Furthermore, plants – like all other organisms – are not only exposed to the natural climatic variability like e.g., annually changes in rainfall caused by the El Niño Southern Oscillation, but also to irreversible anthropogenic caused climatic changes. These changes occur on global scale ('global change') and on local scales e.g., due to habitat fragmentation and creating of new forest edges, and may interrupt the evolutionary evolved phenological processes and – as a consequence – ecosystem functioning (Bawa et al. 1990, Reich 1995). Only few studies have faced this indirect human influence on plant phenology in the tropics, but there is evidence for phenological responses of plants to global change (Chapman et al. 2005, Wright and Calderón 2006) as well as to microclimatic changes due to fragmentation (Laurance et al. 2003, Lovejoy et al. 1986, Restrepo et al. 1999).

Restrepo et al. (1999) detected a higher abundance of fruits of understory trees near new edges compared to the forest interior but this difference vanishes with increasing edge age. Non-uniform responses in phenology to newly created edges are reported by Laurance et al. (2003) for 14 canopy or emergent trees in Amazonia. Only four species show phenological reactions: three of those respond with decreasing flowering or fruiting frequency near the edge, one with increases in fruit and leaf production. The authors suspect higher temperatures and evapotranspiration (i.e., microclimatic changes) near edges to cause a higher physiological stress in some trees, which reduces their reproduction (Laurance et al. 2003).

One reason for the finding of changes in plant phenology due to newly created edges only might be that microclimatic changes decrease at forest edges with increasing edge age. This is a result of changes in vegetation structure of forest edges

with ongoing time caused by increased canopy gap formation near the edge and subsequent regrowth and infilling, which results in a protective layer of dense vegetation (Didham and Lawton 1999, Kapos et al. 1997, Turton and Freiburger 1997).

The forest fragment 'Piedade' is relatively old and its shape (and therefore the edges) has not changed during the last decades. Its edges are nevertheless quite open, since the remnant is surrounded by a cart track that is regularly cleaned manually from outgrowth. Therefore, it is assumed that microclimatic conditions still differ greatly from the forest interior, which might affect the phenology of the common Atlantic Forest tree *Parkia pendula*.

4.3. Material and Methods

4.3.1 Population phenology

The flowering, fruiting, and leafing phenology was documented every calendar week for 20 adult trees in the edge zone and 24 adults in the forest interior (Figure 3; Appendix 1). Observations were carried out from the forest floor with binoculars (Classic II Zoom 8–20 x 50, Konica Minolta Holdings, Japan). The occurrence of the 11 distinguished flowering/fruiting phenophases (3.4.1) was documented for all trees. Not only was the quantitatively dominating phase noted per tree and observation time but also phases that occurred at a lower percentage. For example, if a tree had buds and flowering capitula, the phenophases 3 and 4 were noted independently from the quantitative relation of buds to flowers. Furthermore, the intensities of leaf fall and leaf flush events were scored from zero to four; i.e., either 0, 1–25, 26–50, 51–75, or 76–100 percent of the tree's crown was leafless (Morellato et al. 2000). Additional observations were realized irregularly by climbing into the crowns of most of the observed trees using the single rope technique (Barker 1997). Observation began on September 1, 2003.

Because calendar weeks are scaled circularly (the 52nd week is next to the 1st week of the following year) specific circular statistics (Zar 1999) were necessary to compare the phenological variables between habitats and years. The observed data (phenological variable/individual/calendar week) were transformed into degrees using the following formula:

$$a = (360° \bullet X)/52$$

with X as the calendar week when the phenological variable was observed and a as this week converted into an angular direction (in degrees). The mean angle ($\bar{a}$) and the circular standard deviation (s_0) (Zar 1999) were calculated for all variables per habitat and year. The Watson-Williams test for two samples (Zar 1999) was used to test the null hypothesis that the mean angles ($\bar{a}$) (i.e., the mean dates of the analyzed

phenological variable) were not significantly different for both habitats or the two years of observation. These calculations were carried out for the following phenological variables: a) first nearly ripe buds (begin of phenophase 3), b) first flowers (begin of phenophase 4), c) first pods with gum (begin of phenophase 8), d) begin of defoliation, e) maximum defoliation, and f) newly foliated crowns.

4.3.2 Seed production

During the first investigated flowering/fruiting phase, 2003/04, the number of flowering capitula (phenophase 4), and later, the number of fruit-bearing capitula (phenophase 7) were counted for some branches per tree and afterwards extrapolated for the total crown. The number of pod-bearing capitula per tree was multiplied with the tree-specific mean number of pods per capitulum, which was the mean of 30 randomly chosen capitula per tree. To calculate the number of seeds per tree, the number of pods per tree was multiplied with the tree-specific mean number of seeds per pod. The mean number of seeds per pod was the mean of seeds per pod of 10–20 randomly chosen capitula per tree. In some cases, it was not possible to obtain enough pod-bearing capitula per tree to calculate this variable. The habitat-specific mean of seeds per pod was used in these cases instead. The number of seeds per 100 m² crown area was calculated afterwards to standardize the results. Non-parametrical test and estimates were used due to non-normally distributed variables.

4.4. Results

4.4.1 Population phenology

The flowering pattern of the observed *P. pendula* trees differed considerably between the two years. During the first year of monitoring, 19 of the observed trees flowered both in the forest edge zone and in the forest interior (95.0% and 79.2%, respectively), whereas only three trees in the edge zone (15.8%) and no tree in the interior bore flowers during the second year. However, the rate of defoliated trees was very high and did not differ between both years. During the first observation period, only one tree in each habitat did not change leaves and only one tree in the forest edge zone did not shed leaves during the second year. All observed trees showed a high degree of synchrony in their flowering phenology within a single tree and between trees. The median flowering duration per tree (synchrony within a tree) was 3 ± 1 weeks (n = 38; median ± MAD) in 2003 without differences between the two habitats (Mann-Whitney U: 164.5; p = 0.644). The main flowering period was between the calendar weeks 36 and 46 (3 months) with one tree flowering later during calendar weeks 50 and 51 (Figure 17). The high degree of flowering synchrony within population is displayed in Figure 17. It shows that 25% of all

individuals were in flower during a six-week period (calendar week 38–43) and more than 50% bore flowers within two weeks (calendar weeks 41–42) only.

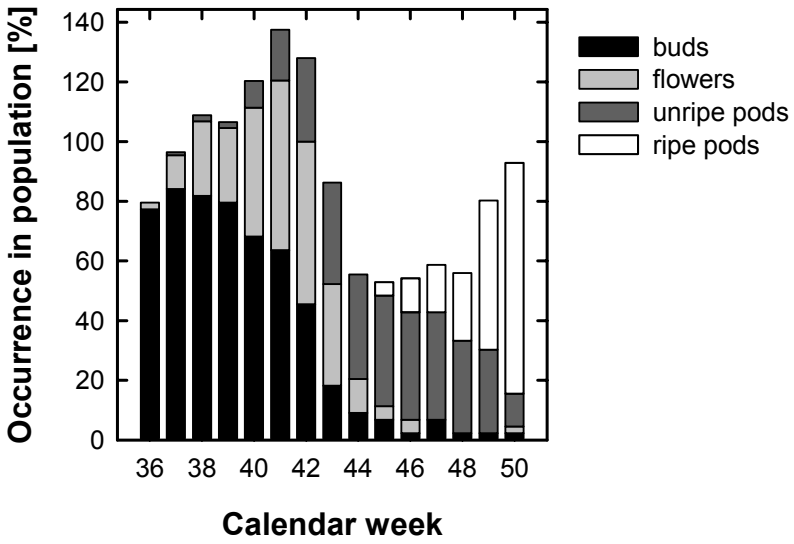

Figure 17 Flowering and fruiting phenology of all *P. pendula* individuals in percent for the flowering period 2003 (accumulation of phases reached more than 100% since all phases which occurred simultaneously at a single tree were taken into account).

The flowering and fruiting synchrony within the total population is also displayed by the lack of significant differences between the two habitats (variables a–c, Table 18). Therefore, the mean dates for these variables are given for the total population only (Table 19). Although the population flowering intensities varied a lot between the two years, no differences in flowering and fruiting date of the three trees, which flowered in both years, were detected between the two years (variables a–c, Table 20).

Table 18 Differences in phenological variables of *P. pendula* between the edge zone and the forest interior.

Period	Phenological variables	F	p
2003/04	a) begin of phenophase 3	2.06	n.s.
	b) begin of phenophase	3.03	n.s.
	c) begin of phenophase 8	0.04	n.s.
	d) begin of defoliation	11.05	< 0.01
	e) maximum defoliation	15.98	< 0.001
	f) newly foliated crown	13.46	< 0.001
2004/05	a) begin of phenophase 3	– [1]	
	b) begin of phenophase	– [1]	
	c) begin of phenophase 8	– [1]	
	d) begin of defoliation	4.88	n.s.
	e) maximum defoliation	3.34	n.s.
	f) newly foliated crown	6.04	< 0.05

[1] = no comparisons could be computed since only three trees in the forest edge zone bore flowers during this period

Table 19 Mean begin of phenological events of *P. pendula* (mean angle ($\bar{a}$) ± circular standard deviation (s_0), and calendar week ± weeks).

Period	Phenological variables	$\bar{a}$ ± s0	Calendar week ± weeks
2003/04	a) begin of phenophase 3	261.83° ± 12.14°	38 ± 2
	b) begin of phenophase 4	277.48° ± 16.59°	40 ± 2
	c) begin of phenophase 8	319.63° ± 12.20°	46 ± 2
	d) begin of defoliation (edge)	353.36° ± 12.82°	51 ± 2
	d) begin of defoliation (interior)	339.03° ± 14.21°	49 ± 2
	e) maximum defoliation (edge)	23.14° ± 8.71°	3 ± 1
	e) maximum defoliation (interior)	355.81° ± 17.81°	51 ± 3
	f) newly foliated crown (edge)	47.72° ± 9.76°	7 ± 1
	f) newly foliated crown (interior)	29.56° ± 19.28°	4 ± 3
2004/05	a) begin of phenophase 3	246.62° ± 28.91°	36 ± 4
	b) begin of phenophase 4	281.54° ± 3.26°	41
	c) begin of phenophase 8	327.69° ± 3.27°	47
	d) begin of defoliation	313.30° ± 15.45°	45 ± 2
	e) maximum defoliation	342.25° ± 19.89°	49 ± 3
	f) newly foliated crown (edge)	14.15° ± 12.81°	2 ± 2
	f) newly foliated crown (interior)	3.84° ± 13.84°	1 ± 2

Despite the fact that there were no differences in flowering and fruiting phenology between the two habitats in 2003/04, leafing phenology differed

significantly (Table 18). All leafing variables (d–f) showed a two to four weeks shift from trees in the forest interior towards trees in the forest edge zone (Table 19, Figure 18). Furthermore, the start of the defoliation process was higher synchronized in the edge zone with 60% of all edge zone trees showing first signs of defoliation during the second week of observed defoliation (Figure 18).

The significant shift towards later leafing events in the forest edge zone was detected during the second vegetation period for new leaves only (Table 18, Figure 18). Although no differences were observed in flowering and fruiting time between the years, all leafing events were significantly earlier during the second year (Table 20, Figure 18).

Table 20 Differences in phenological variables of *P. pendula* between the two years of observation.

Phenological variables	F	p
a) begin of phenophase 3 [1]	1.05	n.s.
b) begin of phenophase 4 [1]	0.89	n.s.
c) begin of phenophase 8 [1]	0.33	n.s.
d) begin of defoliation (edge)	47.38	< 0.001
d) begin of defoliation (interior)	56.90	< 0.001
e) maximum defoliation (edge)	66.10	< 0.001
e) maximum defoliation (interior)	71.44	< 0.001
f) newly foliated crown (edge)	77.94	< 0.001
f) newly foliated crown (interior)	26.33	< 0.001

[1] = only trees which flowered in both years were compared

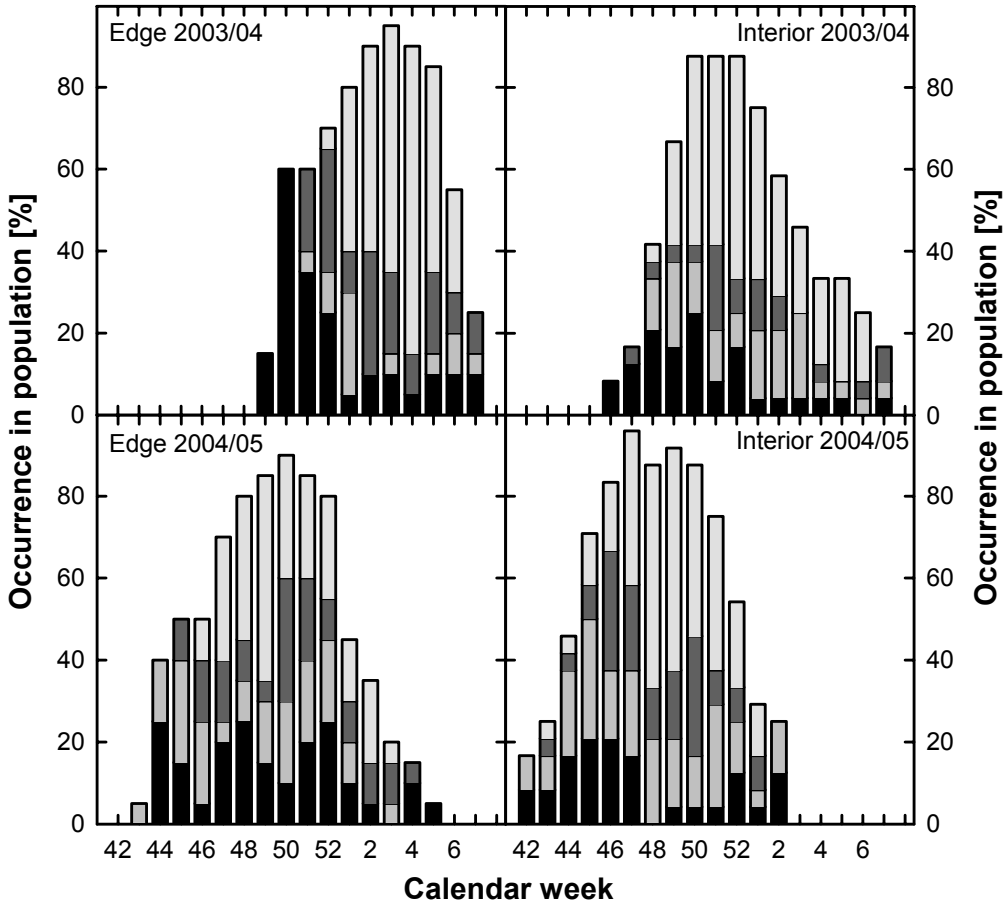

Figure 18 Leafing phenology of the *P. pendula* population in percent (■ = 1-25% defoliated; ■ = 26-50% defoliated; ■ = 51-75% defoliated; ■ = 76-100% defoliated).

4.4.2 Seed production

The median seed production per 100 m² crown area of trees in the forest edge zone was more than 12 times higher compared with forest interior trees. This difference was highly significant despite a high variability within each habitat (Table 21, Figure 19). This difference was not caused by a higher number of seeds per pod or a higher number of pods per capitulum but by a significantly higher number of flowering capitula per tree in the forest edge zone (Table 21).

Table 21 Number of capitula, pods, and seeds of *P. pendula* trees in the edge zone and in the forest interior (2003/04).

		n	Median ± MAD	Min – Max	Mann-Whitney U	p
Capitula (phenophase 4)	Edge	20	1,275 ± 1,107	0 – 3,750		
	Interior	24	216 ± 216	0 – 5,700	122.0	0.005
	Total	44	863 ± 808	0 – 5,700		
Capitula (phenophase 7)	Edge	20	850 ± 738	0 – 2,500		
	Interior	24	144 ± 144	0 – 3,800	122.0	0.005
	Total	44	575 ± 539	0 – 3,800		
Pods/capitulum	Total	38	4.1 ± 0.5	1 – 6	156.5	0.488
Pods (phenophase 7)	Edge	20	4,026 ± 1,418	0 – 12,925		
	Interior	24	521 ± 521	0 – 11,780	113.5	0.003
	Total	44	2,078 ± 2,069	0 – 12,925		
Seeds/pods	Total	27	21.6 ± 1.4	9.8 – 25.7	79.0	0.786
Seeds/tree	Edge	20	80,931 ± 1,418	0 – 291,976		
	Interior	24	11,162 ± 521	0 – 297,563	113.5	0.003
	Total	44	42,361 ± 2,069	0 – 297,563		
Seeds/100 m² crown area	Edge	16	71,575 ± 39,101	0 – 160,981		
	Interior	23	5,789 ± 5,789	0 – 96,299	66.5	< 0.001
	Total	39	38,055 ± 27,230	0 – 160,981		

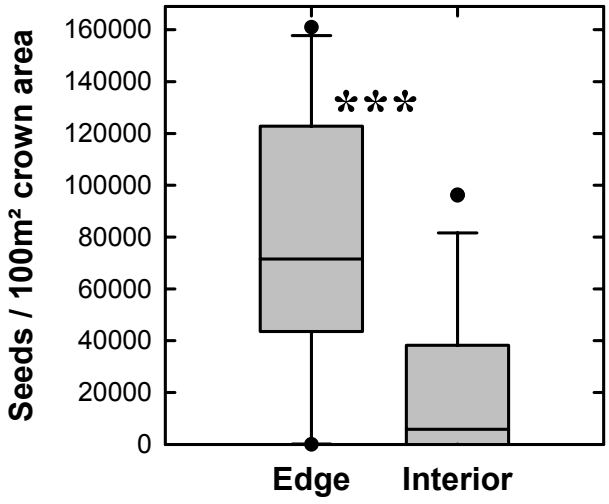

Figure 19 Produced seeds/100 m² crown area of *P. pendula* (2003/04). Edge zone *vs.* forest interior.

4.5. Discussion

4.5.1 Population phenology

The difference in the flowering amplitude of the *P. pendula* population between the two years of observation is remarkable. In 2003, 86.4% (38 trees) of all observed trees bore flowers, in 2004 only 6.8% (3 trees). This pattern cannot be explained with a supra-annual flowering frequency (Newstrom et al. 1994) with the single trees not flowering every year, because all three trees, which flowered during the second year, bore flowers during the first year as well. Furthermore, all present studies which mention the flowering phenology of *P. pendula* assume an annually flowering frequency (Hopkins 1984, 1986a, Peres 2000). Therefore, following Newstrom et al. (1994), the population's flowering pattern can be described as annually with a large variability in the flowering amplitude between the years. Since no difference was found in the beginning date of flowering between the years, the flowering pattern can also be classified to be regularly (Newstrom et al. 1994). Additionally, the individual flowering pattern with its mean flowering duration of 3 ± 1 weeks is a typical cornucopia flowering type (*sensu* Gentry 1974).

The reason for the low flowering amplitude in 2004 might be the very wet pre-flowering period of the respective year. Whereas June 2003 had 311 mm of precipitation, it was nearly doubled in June 2004 with 560 mm. Approx. 300 mm of precipitation is the mean of several years in June, proving that this month was abnormally wet in 2004 (Schessl et al. in press). The earlier leaf shedding during the second year of observation might be another phenological reaction caused by differences in precipitation between the two years. Leaf fall in tropical trees is commonly related with a decline in soil moisture and an increasing water stress for trees (Reich and Borchert 1982). This is obviously also true for *P. pendula* since this species shed its leaves at the end of the dry season, but significantly earlier during the drier and prolonged dry season 2004/05 which was extraordinary dry in all parts of the Atlantic Forest and large areas of the Brazilian interior.

Most probably, the differences in leafing phenology during the first year of observation between the forest edge zone and the forest interior were also related to climatic differences, here microclimatic differences. Due to the relatively open edge vegetation of the forest fragment 'Piedade', its soil moisture is expected to by drier than in the forest interior (Kapos et al. 1997, Turton and Freiburger 1997) which commonly results in a higher water stress for plants and therefore leaf shedding (Reich and Borchert 1982). This is confirmed on-site in the 'Piedade' fragment by an overall higher litterfall during the dry season and a higher litterfall in the forest edge zone compared with the forest interior (Schessl et al. in press). Nevertheless, the leaf

fall of *P. pendula* started highly significantly earlier in the forest interior than in the edge zone in 2003. The most likely reason for this surprising edge effect can be found in the surrounding cultivation of sugarcane. Harvest time started with the beginning of the dry season. All fields were heavily irrigated for about two weeks (with liquid residua from the industrial sugar production) after the sugarcane had been harvested to facilitate the new sugarcane sprouting. The adjacent forest edge vegetation was often within the range of the sprinklers and the resulting water flow on the dry topsoil frequently drained into the forest edge zone. This artificial water supply obviously raised the soil moisture considerably in the forest edge zone and resulted in a delayed leaf shedding of the *P. pendula* trees in 2003. The dry season in 2004/05 was perhaps too harsh and prolonged to result in a later leaf fall in the edge zone due to the additional water.

The lesser flowering in 2004 (also observed by Hopkins (1981) in Amazonia for the flowering period 1979 compared with 1978), the earlier leaf shedding in 2004, and the delayed leaf fall in the forest edge zone in 2003 show most properly the high sensibility of *P. pendula*'s flowering and leafing phenology to interannual climatic variability and microclimatic patchiness. Furthermore, it shows the importance of long-term phenological surveys to reveal sound phenological patterns which are indispensable to verify the here presented interpretations.

4.5.2 Seed production

The number of seeds per pod and pods per capitulum did not differ between the two habitats. Differences in these variables are regularly found if the pollination process of self-incompatible plant species (like *P. pendula*) is disturbed either by a reduced number of pollinators (Ågren 1996, Jacquemyn et al. 2002) or by a reduced number of transferred pollen (Cunningham 2000a, Knight 2003). Thus, the enormous difference in seeds per crown area cannot be explained with pollen- or pollinator-limitation, which often occurs as a result of habitat fragmentation (Ågren 1996, Cunningham 2000a, Jacquemyn et al. 2002, Knight 2003, Murcia 1993). The sufficiently running pollination process in *P. pendula*, being unaffected by fragmentation effects, can be explained by the relatively high number of its individuals in the fragment (Guedes 1998) and by the behavior of its main pollinator. *Phyllostomus discolor*, which was highly attracted by the blossoms and transferred large pollen loads, is known to fly large distances per night, most probably in huge flocks (Heithaus et al. 1975). The distances of several dozens or hundreds of meters between the trees in the edge zone and the forest interior or between neighboring fragments are hence no obstacle for the pollinators, which are therefore efficient pollinators of *P. pendula* even in fragmented landscapes.

The much higher number of seeds per crown area in the edge zone was a result of the higher number of flowering capitula per tree in this habitat. Even though the variability of blossoms per tree within each habitat was very high, the difference in flower production was highly significant. Similar results were found for the shrubs *Senna artemisioides* (Caesalpiniaceae) and *Eremophila glabra* (Myoporaceae) in Australia (Cunningham 2000b). Cunningham (2000b) speculated that this difference is a result of higher irradiance, less competition for water due to a lighter vegetation, or a higher soil nutrient content at the edge. Another possible explanation in the case of *P. pendula* at the Usina São José could be the influx of water and nutrients from the surrounding heavily fertilized sugarcane fields, which is a known anthropogenic induced abiotic edge effect (Murcia 1995). Whichever of these factors or a combination of them is the proximate factor for the higher flower production of *P. pendula* in the edge zone of the forest fragment 'Piedade', it is clear that the flower production is another event in the phenology and reproduction of this tree species that is heavily influenced by edge effects.

5. Seed Fate of *Parkia pendula* in the Absence of Primary Dispersers – Forest Edge Zone *vs.* Interior

5.1. Abstract

The fate of *Parkia pendula* seeds that lacked primary dispersal by primates was experimentally investigated on the forest floor in the forest edge zone and interior of an Atlantic Forest remnant in Pernambuco, Brazil. Effects of seedpod exudate attached to the seeds were also considered. Additionally, the ant fauna of the two habitats was determined by pitfall traps. Seeds on the forest floor disappeared in the forest interior significantly faster from the seed stations than seeds in the edge zone. Their median survival time was 9 and 21 days, respectively. The effect of attached seedpod exudate was also significant. The median survival time of seeds with gum was 21 days and 3 days for seeds without gum, regardless of their distance to the forest edge. Seed removal by scatterhoarding rodents can be excluded as explanation and on-site predation by ants counted only for approx. 8% of the seed loss. Therefore, seed removal by ants is assumed to be mainly responsible for the disappearance of seeds from the stations. 397 individuals of 42 ant species were trapped in 20 pitfalls. The ant assemblages showed a high species overlap between the two habitats. Nevertheless, the foraging area of the most abundant seed dispersing ant *Pachycondyla crassinoda* was clearly shifted towards the forest interior and may therefore explain the strong edge effect on seed removal.

5.2. Introduction

Seeds are the result of sexual reproduction in vascular plants and bear an embryo within. Their small size and large number determines them to be the principle means by which plants move across landscapes (Vander Wall et al. 2005a). The necessity for seed dispersal is founded in a higher risk of predation and parasitism near the parent tree, parental and sibling competition (Janzen 1971) and sometimes inappropriate germination and growth conditions (Willson 1992). Since seeds are primarily immobile, their dispersal has to be performed by abiotic forces (e.g., wind), by ballistic features of the fruits of some species, or by animals. In most cases of zoochorous primary dispersal, adaptations of the fruit facilitate the dispersal process either by structures that attach the fruit at the animals' body (epizoochory) or mainly by nutritional rewards for feeding animals, which thereby unintentionally swallow the seeds and defecate or spit them afterwards (endozoochory). Endozoochory is by fare the dominating dispersal-syndrome in the tropics (Jordano 1992) and vertebrates are the main animal vectors since 45–90% of all tropical plants are supposed to be adapted to vertebrate dispersal (Garber and Lambert 1998).

Beside the first seed movement (primary dispersal) there is often another movement following (secondary dispersal) mediated by other vectors. The principle

groups of secondary dispersers are scatterhoarding rodents, ants, and dung beetles (Vander Wall and Longland 2005). This two-phase dispersal is called diplochory (van der Pijl 1969). Most studies on seed dispersal of tropical plants focused on primary dispersal, only recently the importance of secondary seed dispersal for the seed fate and plant demography have been emphasized (Pizo et al. 2005, Vander Wall et al. 2005b). Another reason for the growing importance is the negative human impact on vertebrate populations. Vertebrate populations decline or even get extinct locally due to hunting and habitat destruction (Bonaudo et al. 2005, Cullen Jr et al. 2000), what again changes the vegetation composition and even hinders the regeneration of some plant species due to the loss of dispersers (Forget and Jansen 2007, da Silva and Tabarelli 2001, Wright 2003). In some cases, secondary seed dispersers of unhunted groups like ants may compensate the loss of primary disperser to some percentage (Guimarães Jr and Cogni 2002) even if their dispersal distances are much shorter (Stiles 1992). But even ant-seed-interactions may be anthropogenically affected, e.g., by edge effects in forest fragments (Guimarães Jr and Cogni 2002).

The seedpod exudate of *P. pendula* is known to be very attractive as a source of nourishment for a wide range of arboreal vertebrates, mainly of primates (Peres 1994, 2000). Most probably, the primates swallow the seeds while feeding on the gum and defecate them thereafter, such as proved for *Parkia panurensis* (Knogge et al. 2003, Knogge and Heymann 2003). The only primate that occurred in the study area, *Callithrix jacchus*, fed heavily on the seedpod exudates of *P. pendula*, as was observed in the field and during feeding experiments with captive individuals. Beside this presumed mutualistic behavior, the primates were also observed feeding on the exudate during the weeks before pod opening being therefore herbivores as well. All other primates, known to occur in this region like e.g., *Alouatta belzebul* or *Cebus* sp. (Almeida et al. 1995, Monteiro da Cruz and Campello 1998) were already locally extinct in the studied forest fragment 'Piedade', most probably as a direct or indirect effect of hunting and habitat destruction.

Although *C. jacchus* was still present in the studied fragment, many of the *P. pendula* trees were not located within any of the small foraging areas of the primate groups (home range size: 0.7–6.5 ha; de Castro 2003, Scanlon et al. 1989) and lacked therefore any primary seed disperser. Furthermore, an overall very lower number of *C. jacchus* groups in the forest fragments of the Pernambuco endemism center was recently shown by Mendes Pontes et al. (2007). Seeds, which were not ingested by arboreal vertebrates, often stayed for months attached to the exudate (3.4.1) before they dropped to the forest floor either with still some gum attached or gum-less if the water-soluble exudate was washed off by rain. On the forest floor, ants were observed predating these seeds but also removing them. The following questions

arose from these observations: How high is the removal rate of *P. pendula* seeds on the forest floor? Is this affected by the seeds' relative position to the forest edge? If so, are there any differences in the leaf-litter ant fauna that could explain this pattern? Furthermore, is there any effect of attached gum on the removal rate? These questions are somehow crucial questions and of some conservational interest since *P. pendula* is one of the most common trees of the Atlantic Forest of the Pernambuco region (Ferraz et al. 2004, Guedes 1998) and its regenerative organs are discussed to be a keystone resource for the regional mammals fauna (3.5.6).

5.3. Material and Methods

5.3.1 Seed dispersal/predation

The fate of *P. pendula* seeds after dropping on the forest floor was experimentally investigated. Twenty seeds were arranged each at ten positions in the forest edge zone and ten positions in the forest interior. The distance between each 50 cm x 50 cm seed station and the minimum distance to the nearest fruiting *P. pendula* tree was approximately 10 m. The 20 seeds per station were arranged in four rows with five seeds each. The seeds of the first and third row had never been in contact with the seedpod exudate, whereas the seeds of the second and fourth row were artificially covered with seedpod gum, quantitatively corresponding to observations made underneath fruiting *P. pendula* trees. Before the arranging of the seeds, the uppermost litter layers were manually removed. The position of each seed was marked with a woody toothpick. The experiment started on December 12, 2004, and run 30 days with a control every three days. Parallel running experiments at the same locations with seeds in small, sand-filled bowels, which were placed within larger bowls filled with water proved that no vertebrates were feeding on *P. pendula* seeds on the forest floor at the study site. Feeding on the larger seeds of *P. panurensis* was shown for scatterhoarding rodents previously (Feldmann 2000, Feldmann et al. 2000).

Seed loss due to removal or totally predation on site was categorized as 'event' in the calculated Kaplan-Meier survival analysis. This analysis was performed using SigmaStat 3.5 (Systat Software Inc. 2006). The survival time was set to one day for seeds, which disappeared between the start of the experiment and the first census three days later, since a zero is interpreted as missing data by the software.

5.3.2 Ant assemblages

To survey the ant litter fauna, pitfall traps were installed at the 10 sites in the forest interior and the 10 sites in the forest edge zone where seed removal was previously examined (5.3.1). The internal diameter of the traps was 75 mm and they were filled

with approx. 50 ml ethanol and a drop of detergent (Bestelmayer et al. 2000). The traps were installed on March 23, 2005, and were run for 48 h (Agosti and Alonso 2000). All ant material from the traps was mounted and identified thereafter by Ana Gabriela Delgado Bieber from the myrmecology group of the Universidade Federal de Pernambuco (UFPE), where the specimens were also deposited.

The species accumulation curve, ß-diversity indices, and species richness estimators were calculated by the computer package EstimateS 8.0 (Colwell 2006) after randomizing the data 1,000 times. To calculate the species overlap between the samples in the forest edge zone and the forest interior, the new Chao's Jaccard abundance-based similarity index ($\hat{J}_{abd}$), which is corrected for unseen species (Chao et al. 2005), was calculated beside the classic Jaccard similarity index (J_{clas}). The new index is much more valuable for samples that are suspected to be undersampled, very diverse, and to contain numerous rare species (Chao et al. 2005).

5.4. Results

5.4.1 Seed dispersal/predation

The differently treated seeds differed significantly in their median survival times (Table 22). There was a clear 'exudate-effect': the seed loss curves of seeds without gum were all negative logarithmic: high seed losses of over 50% during the very first days followed by a relatively low disappearance rate until the end of the experiment (Figure 20 a, Figure 21). Contrary, the disappearance rates of seeds with gum were all linear, i.e., the seed loss was more or less constant over the 30 days lasting experiment. The gum was that sticky that it was a deadly trap on the forest floor for invertebrates as well as for some small crawling vertebrates (Figure 22).

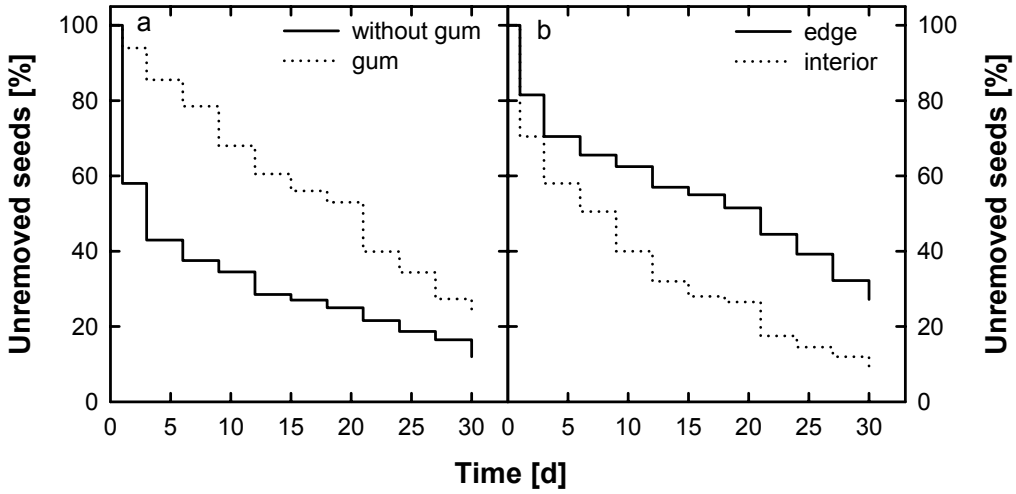

Figure 20 *P. pendula* seeds on the forest floor. a: gum *vs.* without gum; b: forest edge zone *vs.* interior.

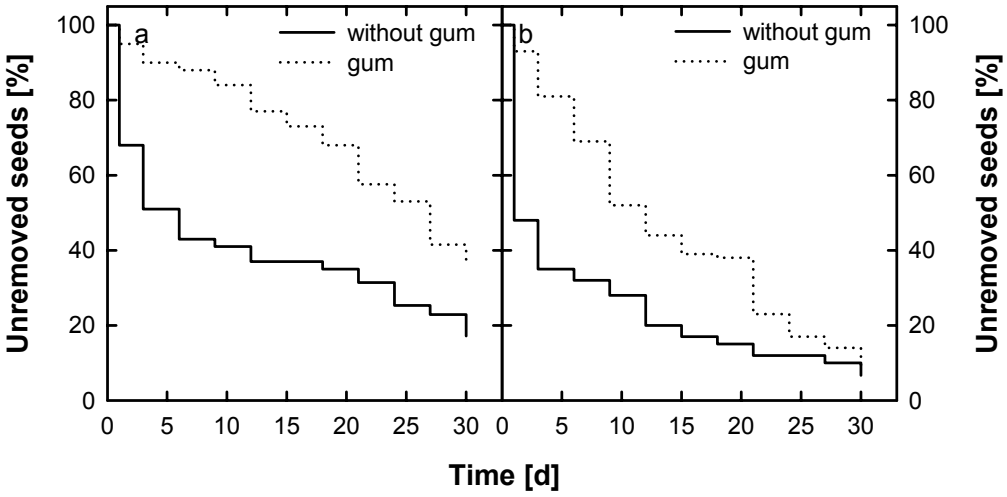

Figure 21 *P. pendula* seeds on the forest floor in the (a) forest edge zone and (b) in the forest interior.

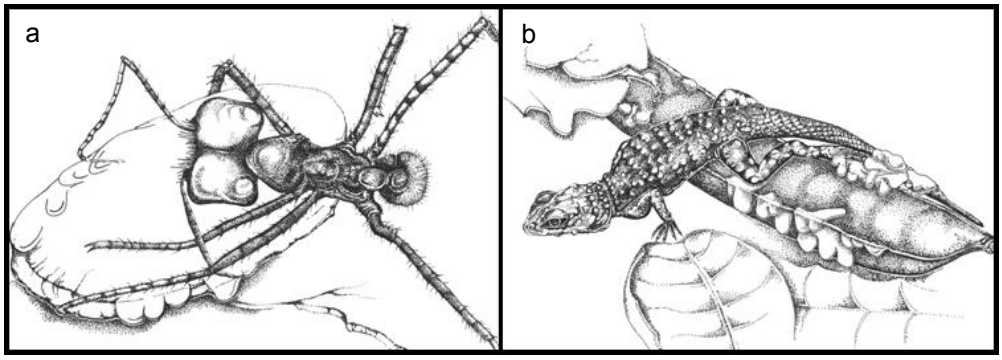

Figure 22 *P. pendula* seedpod exudate as deadly trap for animals on the forest floor. a: *Atta* sp. glued to a *P. pendula* seed; b: lizard glued to a *P. pendula* pod. (Illustrations by J. Piechowski after photographs).

Beside the 'exudate-effect', there was a clear edge effect, too. Seeds in the forest interior disappeared much faster from the seed stations than seeds in the forest edge zone. This difference held true for seeds with and without gum (Figure 20 b, Figure 21). Therefore, the largest differences were observed between gum-less seeds in the forest interior and seeds with gum in the forest edge zone with a median survival time of < 3 and 27 days, respectively (Table 22).

Table 22 Median survival times of *P. pendula* seeds on the forest floor. Forest edge zone *vs.* interior and seeds with gum *vs.* seeds without gum.

		n	Median [d]	25/75 percentile [d]	Log-Rank statistic	p
All	Edge	200	21	- */ 3	33.699	<0.001
	Interior	200	9	21/<3		
	Without gum	200	3	18/<3	35.884	<0.001
	Gum	200	21	30/ 9		
Edge	Without gum	100	6	27/<3	22.756	<0.001
	Gum	100	27	- */ 15		
Interior	Without gum	100	<3	12/<3	15.461	<0.001
	Gum	100	12	21/ 6		

* = more than 25% were still present at the seed-station at the end of the study.

6.1% and 10.5% of all disappeared seeds in the edge zone and forest interior showed predation-marks during prior controls. This rate was 9.1% for seeds with gum and 8.2% for the gum-less seeds. In most cases, these herbivores were small ants, which fed on the endosperm of the seeds.

5.4.2 Ant assemblages

In total, 397 ant individuals of 42 species were trapped in the 20 pitfalls. The number of individuals in the forest edge zone was visibly higher than in the forest interior, but the species number was equal (Table 23). The classic Jaccard similarity index (J_{clas}) displays two rather different leaf-litter ant faunas with a species overlap of 43%. Nevertheless, the $\hat{J}_{abd}$ index, which is much more sensitive for rare species and takes also the unseen species into account (Chao et al. 2005), shows a high species overlap of 83% between the two habitats (Table 23).

Table 23 Number of individuals, species, singletons, uniques, shared species, and ß-diversity indices for the leaf-litter ant fauna in the edge zone and the forest interior (J_{clas}: classic Jaccard overlap index; $\hat{J}_{abd}$: Chao's abundance-based Jaccard index).

	Traps	Individuals	Species	Singletons	Uniques	Shared species	J_{clas}	$\hat{J}_{abd}$
Edge	10	142	30	14	18			
Interior	10	255	30	12	19	18	0.429	0.826
Total	20	397	42	15	20			

Because of the hardly existing faunal change between the two habitats, indicated by the $\hat{J}_{abd}$ (Table 23), it is referred hereafter as one single ant community. The 42 detected ant species represent a quite good sampling efficiency. The mean estimated number of species is 63, wherefore the sampled species display a sampling efficiency of 66.7% of the expected number of species (Table 24). This overall

species covering is also displayed by the sample-based species accumulation curve, which is getting flatter toward its end (Figure 23).

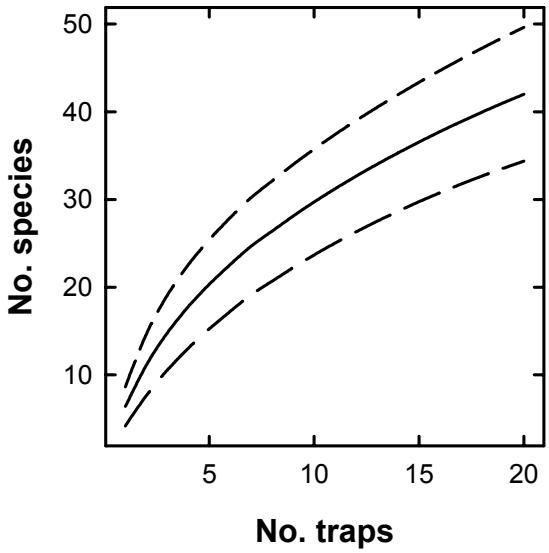

Figure 23 Sample-based interpolated species accumulation curve for the total forest fragment's leaf-litter ant fauna (solid line: expected species richness values; dashed lines: 95% confidence intervals).

Table 24 Total ant species numbers calculated by different species richness estimators (rounded). Sampling efficiency (percentage of observed divided by estimated species number) is given in brackets.

Observed	ACE	ICE	Chao1	Chao2	Jack1	Jack2	Bootstrap	MMMean	Mean
42	63 (66.7)	74 (56.8)	55 (76.4)	67 (62.7)	61 (68.9)	72 (58.3)	50 (84.0)	59 (71.2)	63 (66.7)

Beside the high similarity on community level between the two habitats, there were some clear differences on species level between the forest edge zone and the interior. Especially the foraging area of the largest ant species, *Pachycondyla crassinoda* (body-length: 16 mm), was clearly shifted towards the forest interior in abundance as well as occurrence in traps. Only one individual was found in a trap in the forest edge zone, whereas this species was found in all ten pitfalls in the forest interior with a mean of approx. seven individuals per trap (Table 25). Other species tended to be more abundant in the forest edge zone (e.g., *Paratrechina* sp. 2), but no other species showed such a clear pattern like *P. crassinoda*, apparently partly because no other species was so abundant (Table 25).

Table 25 Abundance and incidence list of the leaf-litter ant fauna in the forest edge zone and interior.

	Edge		Interior		Total	
Species	Traps	Individuals	Traps	Individuals	Traps	Individuals
Acromyrmex sp. 1			1	2	1	2
Acropyga sp. 1	1	1			1	1
cf. *Acropyga*	1	3			1	3
Apterostigma sp. 1	1	1	1	1	2	2
Apterostigma sp. 2			1	1	1	1
Atta cephalotes	2	22	1	5	3	27
Atta sexdens	1	1			1	1
Camponotus sp. 1			1	1	1	1
Crematogaster sp. 1	2	3	5	11	7	14
Cyphomyrmex sp. 1	1	1	1	1	2	2
Ectatomma sp. 1	4	5	3	3	7	8
cf. Formicinae			1	1	1	1
Gnamptogenys sp. 1			4	8	4	8
Hypoponera sp. 1	2	2			2	2
Leptogenys sp. 1			1	1	1	1
Mycocepurus sp. 1	1	1	1	1	2	2
Odontomachus sp. 1	1	1	1	1	2	2
Oligomyrmex sp. 1	1	1			1	1
Pachycondyla crassinoda	1	1	10	69	11	70
Pachycondyla sp. 2	5	10	6	34	11	44
Paratrechina sp. 1	1	2	2	2	3	4
Paratrechina sp. 2	4	16	1	2	5	18
Pheidole sp. 1	2	2			2	2
Pheidole sp. 2	1	1			1	1
Pheidole sp. 3	5	21	1	8	6	29
Pheidole sp. 4	6	9	3	9	9	18
Pheidole sp. 5			2	5	2	5
Pheidole sp. 6	3	6	4	16	7	22
Pheidole sp. 7	1	4	5	32	6	36
Pheidole sp. 8			1	5	1	5
Pheidole sp. 9	1	16			1	16
cf. *Pheidole*	1	1			1	1
Ponerinae sp. 1			1	1	1	1
Pseudomyrmex sp. 1	1	1	1	1	2	2
Sericomyrmex sp. 1	3	5	7	26	10	31
Sericomyrmex sp. 2			1	1	1	1
Solenopsis sp. 1	2	2	1	4	3	6
Solenopsis sp. 2	1	1			1	1
Strumigenys sp. 1			1	1	1	1
Tapinoma sp. 1	1	1			1	1
Trachymyrmex sp. 1			1	2	1	2
Trachymyrmex sp. 2	1	1			1	1

5.5. Discussion

5.5.1 Seed dispersal/predation

The reason for the 'exudate-effect', i.e., seeds with exudate were removed to a smaller degree than seeds without, can be explained by the exudate itself: it was very sticky. The seeds were glued to the substrate by the exudate, being therefore less portable for the ants. Its stickiness was probably due to its high content of

polysaccharides of the main constituent sugars galactose and arabinose (Anderson and de Pinto 1985, Peres 2000). A combination of these carbohydrates with the 2.2–3.1% protein content (Anderson and de Pinto 1985, Peres 2000) to glycoproteins is unknown but very likely since these compositions are often found to be the basis of naturally occurring glues (Onusseit 2004). These organic glues are similar to synthetic glues in their 'gluing-performance' (Onusseit 2004). This gluing performance of *P. pendula* gum is that good and its quantity that high (6.34 ± 2.79 g per pod; unpubl. data), that it is used for catching birds (Hopkins 1986a) and may become a deadly trap on the forest floor for invertebrates as well as for small crawling vertebrates. Ants, which tried to move seeds with attached gum, were observed several times at the seed-stations. In most observed cases, they were unsuccessful and they often stuck to the exudate and died. The reason for the seeds' attractiveness for the ants is still unknown. Maybe, the sugar-rich gum played a role but the gum-less seeds were also attractive to them. The lipid-rich cotyledons (Gonçalves et al. 2002) were certainly very attractive since a proportion of the seeds was predated on-site by small ants like *Pheidole* sp. and probably also *Sericomyrmex* sp. (Feldmann et al. 2000). Nevertheless, only 8 ±2% of all seeds showed signs of granivory before they disappeared and most of these predation processes of single seeds were observed during successive controls, i.e., this process lasted longer than three days. This coincides with the mean predation duration by insects – mainly *Sericomyrmex* sp. – of 5.9 ± 3.6 days (n = 17) on the larger seeds of *P. panurensis* (Feldmann 2000). Therefore, it is doubtfully to explain a larger percentage of seed-loss with on-site granivory to interpret the attractiveness of gum-less seeds.

Direct observations of seed removing *Atta* sp. and especially *Pachycondyla crassinoda* were made irregularly during the controls. The large ants of the genus *Pachycondyla* are single foraging specialist predators of other arthropods (Andersen 2000, Brown Jr 2000) but also important and frequent seed dispersers in different Neotropical habitats (Horvitz and Schemske 1986, Passos and Oliveira 2003, Pizo and Oliveira 2001). However, other than in the *P. pendula* case, the diaspores so fare known to be removed by *Pachycondyla* sp. were all fleshy. The ants feed on the fleshy pulp or aril and deposit the cleaned viable seeds on refuse piles outside their nests (Pizo and Oliveira 2001). The fate of *P. pendula* seeds removed by *P. crassinoda* is completely unknown. Do the ants feed on the gum and leave the seed unharmed (dispersal)? If so, why did they remove gum-less seeds? Alternatively, do they predate the seeds after removing them? To clear these questions, the exact seed fate of single seeds has to be studied in detail in the forthcoming project phase using video monitoring (Jansen and den Ouden 2005) and seed tracking methods (Forget and Wenny 2005). Only after these studies, the seed removal of *P. pendula* can be

appropriately interpreted and the benefit or cost for the plant species properly calculated (Vander Wall et al. 2005b).

The temporal pattern of disappearance of seeds without gum matched the theoretical considerations: a high rate at the beginning, when seed density was high and a declining rate with declining seed densities with ongoing time ('density-responsive' of predators, pathogens, dispersers, and competition: Janzen 1971). However, the disappearance rates of seeds with gum were all more or less constant. This could be interpreted as a time and density autonomy, what highly contradicts the density (and therefore time) dependent disappearance rates of seeds without gum. However, this contradiction can be cleared after analyzing this process more deeply. The removal rate of seeds with gum was very low at the beginning of the experiment due to the gluing effect of the exudate. Nevertheless, some seeds were removed even then wherefore the seed density was slowly reduced. However, a lower removal rate was not the result of this lower seed density. The seeds became more movable with ongoing time since the gum was slowly washed off the seeds by rain. Therefore, the effect of the declining seed density on the removal rate was abrogated by the raising seed ability to be transported by ants. The annulment effect of these two processes led to a constant disappearance rate over the 30 days lasting experiment.

The only thinkable reason for the edge effect on the removal rate is a difference in removal agents, i.e., there were either less seed removing species in the forest edge zone or the abundance of these species was lower or they behaved differently than in the forest interior. Three different animal groups are regularly secondary seed dispersers: scatterhoarding mammals, dung beetles, and ants (Vander Wall and Longland 2005). Mammals do not come into consideration to explain the seed removal patterns since they obviously were not attracted by the seeds. All the seeds at the seed stations which were nearly impossible to reach for arthropods (because these seeds were surrounded by a shallow trench filled with water) but easily accessible for mammals, were completely unharmed during the experiment. Dung beetles can be excluded from the consideration, too, because they are either interested in vertebrate faeces or fleshy fruits (Andresen and Feer 2005, Gottsberger and Silberbauer-Gottsberger 2006b). Therefore, only a change in the ant community, different abundances of ant species or differently behaving ant species are possible explanations for the observed differences in seed removal rates between the forest edge zone and the forest interior.

5.5.2 Ant assemblages

The recorded 42 ant species display 30–49% of the leaf-litter ant fauna discovered in remnants of the Atlantic Forest so far with a much higher technical and temporal

effort (Delabie et al. 2000, Majer et al. 1997, Schoereder et al. 2004, Silva et al. 2007). Nevertheless, pitfall traps are a little time-consuming, self operating method to investigate the epigaeic ant fauna (Bestelmayer et al. 2000), the species which are most likely seed dispersers/predators. Therefore, and because 57–84% of the estimated ant species, which can be caught with this method, were trapped, one can conclude, that the outcome of this study is at least a valuable first image of the occurring leaf-litter ant fauna of the 'Piedade' forest.

Even with the larger sampling effort, Majer and colleagues (1997) could not detect any clear edge effects on the litter-dwelling ant fauna in the Atlantic Forest. They concluded that 'a forest-like ant fauna is able to persist right up to the interior edge of the forest' (Majer et al. 1997) although there was evidence that species richness was highest in the forest interior (Majer et al. 1997). Nevertheless, there is also evidence that the interactions between ants and non-myrmecochorous diaspores are affected by edge effects as Guimarães Jr and Cogni (2002) showed in the Atlantic Forest of São Paulo state. Seed cleaning of *Cupania vernalis* (Sapindaceae) is significantly higher in the forest interior (Guimarães Jr and Cogni 2002). These two results seem to be contradictorily but were perfectly reflected by the findings of the present study: a high species overlap between the forest edge zone and the forest interior but a clear, significant difference in seed dispersal.

An explanation for the unsuspected similarity in the ant fauna of edge and interior could be the common occurrence of treefall-gaps within the forest interior in the study by Majer et al. (1997) and also in the present study. Even small gaps change factors which are important for the ant distribution like e.g., the soil moisture on a small scale (Clinton 2003). These changes could be a reason for small-scale occurrence of species adapted to different habitats. This small-scale heterogeneity might therefore be the reason that no differences on a broader scale (edge *vs.* interior) were detectable in the ant community composition. Nevertheless, there were differences on species-scale beside the similarity on community-scale. The clearest difference in abundance and occurrence in traps was found for the largest and most abundant ant species, *P. crassinoda*. The foraging area of this species was obviously shifted towards the forest interior. Since this ant genus is known to be an important and abundant seed disperser (Horvitz and Schemske 1986, Passos and Oliveira 2003, Pizo and Oliveira 2001) and this species was irregularly observed removing *P. pendula* seeds, the spatial pattern of this species was possibly the reason for the observed edge effect on seed removal. An analysis of the ant community composition might therefore be inappropriate to explain differences in plant-ant-interactions.

6. Germination, Seedling Establishment, and Population Structure of *Parkia pendula* – Forest Edge Zone *vs.* Interior

6.1. Abstract

Germination, seedling establishment, and the population structure of *P. pendula* were studied in relation to the distance to the forest edge in a fragment of the northeastern Brazilian Atlantic Forest in order to determine edge effects. Germination and seedling survival was observed underneath adult trees in the edge zone and the forest interior; the population structure was examined in transects with a total area of 1 ha in each habitat. The overall germination rate was very low but significantly higher in the forest interior than in the edge zone (0.52% *vs.* 0.21%). Furthermore, the seedlings' survival time was significantly longer in the forest interior. The probability to survive the first nine months after germination was three times higher in the forest interior. The higher germination rate and the better seedling establishment in the forest interior are suspected to be the reasons for the significantly higher seedling density within the forest interior. However, the larger size classes did not follow this pattern. The sapling density was equal in both habitats but the density of juvenile trees was three times higher in the edge zone.

6.2. Introduction

Parkia pendula is a typical (de Andrade-Lima 1960, Ferraz et al. 2004, Siqueira et al. 2001) and abundant (Guedes 1998, Lins-e-Silva 1996, Siqueira et al. 2001) species of the Atlantic Forest endemism center of Pernambuco (Cardoso da Silva and Casteleti 2003). Its density in this region is much higher than in the Amazonian forests (Peres 2000, M.J.G. Hopkins pers. comm.).

The results published so far about the germination ability and survival rates of *P. pendula* differ widely. First attention was paid to the germination of *P. pendula* seeds by Rizzini (1977). He stated that the seeds "refuse to germinate under any experimental set of conditions" including e.g., mechanical scarification. Similar observations were made by Teppner (pers. comm.). Contrary, Alencar and Magalhães (1979) obtained a germination rate of 58.5% using untreated seeds. Barbosa et al. (1984) tested different pre-germination treatments and got germination rates of approx. 70% with different methods of mechanical and chemical scarification. Scarano and Crawford (1992) even obtained a germination rate of 80%. All these studies used a similar high number of repetitions and time spans for their germination tests. Beside these laboratory germination tests, germination of *P. pendula* seeds was also tested in comparable field studies. Camargo et al. (2002) directly sowed the seeds after mechanical scarification at undisturbed forest, secondary vegetation, pasture, and bare soil sites. Germination rate was high at the bare soil transects (approx. 70%), but low at the other three sites (approx.

15%, 5%, 0%, respectively). Germination tests by Schulze (2003) in logging gaps and neighboring close forests revealed an "overall extremely low germination rate for *P. pendula*" of 4.6%. Furthermore, he found no significant difference in germination rates between untreated and manually scarified seeds. Shoot growth was vigorous and survival rate greater than 75% during the first two years after planting of *P. pendula* seedlings at open reforestation sites (Knowles and Parrotta 1995). Contrary, only ~25% of the *P. pendula* seedlings on bare soil sites survived the first year whereas the seedlings at forest and secondary forest sites died within this period (Camargo et al. 2002).

Distance to forests edges is known to have an enormous influence on the seed production of *P. pendula* trees (4.4.2) as well as on the secondary dispersal of *P. pendula* seeds by ants (5.4.1). These two processes in a plant's "seed dispersal cycle" (Wang and Smith 2002) are crucial for the following processes of germination and recruitment and therefore seedling distribution (Wang and Smith 2002). The verified differences due to edge effects on *P. pendula* could be imparted from the pre-germination level to the next levels up to population structure. Beside these already proved edge effects, germination and recruitment itself are known to be influenced by factors that are altered by forest edges, like the quantity and quality of irradiance, soil moisture, litterfall, and pathogen damage (Asbjornsen et al. 2004, Benítez-Malvido and Lemus-Albor 2005, Bloor and Grubb 2003, López-Barrera and Newton 2005, Pearson et al. 2003, Schessl et al. in press, Sizer and Tanner 1999).

The goal of this study was to determine possible differences in germination and seedling establishment and as a consequence in population structure of *P. pendula* between sites in the forest interior and in the forest edge zone.

6.3. Material and Methods

6.3.1 Germination and seedling establishment

In early February 2004, approx. one month after seedpod opening, 32 circular plots (diameter: 6 m; area: 28.27 m^2) were installed underneath the crowns of fruit-bearing *P. pendula* trees in the edge zone and the interior of the forest (14 and 18 trees respectively; trees D007, D013, D014, D015, D016, D018, D020, D021, D022, D024, D025, D117, D118, D120, D122, D123, D124, D125, D126, D131, D132, D133, D134, D135, D136, D161, D163, D164, D167, D180, D181, 812; Appendix 1). All *P. pendula* seedlings within the plots were marked individually with colored wooden spikes. Monthly, number of leaves per seedling and total number of seedlings per plot were counted and new sprouted seedlings were marked. The last counting was in December 2004, right before the release of new seeds.

All variables were calculated for a standard area of 100 m² per tree and were set into relation to the number of produced seeds per 100 m² crown area (4.4.2) to calculate a comparable germination rate per tree. Therefore, the here used term 'germination rate' is the percentage of germinated seeds underneath the mother-tree per produced seeds, calculated for equal areas. This calculation of germination rate ignores primary as well as secondary seed dispersal and predation and is therefore somehow simplified.

Since the data were not normally distributed (Shapiro-Wilk-test of normality), the non-parametrical Mann-Whitney U test was used to detect differences between the two habitats using the software-package SPSS for Windows 11.0 (SPSS Inc. 2001). The seedling survival time was calculated using the Kaplan-Meier survival analysis. The survival time was set to a half month for seedlings, which were not detected the month after their first registration, since a zero is interpreted as missing data by the software. Fisher's exact test was used to analyze the leaf growth between the habitats. The Kaplan-Meier survival analysis and Fisher's exact test were performed using SigmaStat 3.5 (Systat Software Inc. 2006).

6.3.2 Population structure

Ten 20 m x 50 m transects were installed each in the forest edge zone and in the forest interior of the forest fragment 'Piedade' in March 2005. All transects were subdivided into ten 10 m x 10 m plots. The transects' longitudinal sides were arranged parallelly to the forest edge. The diameter at breast height (dbh) of all *P. pendula* individuals >2 m in height was calculated after measuring the circumference at breast height following Condit (1998); the tree height was estimated. The root collar diameter (rcd) and height of all *P. pendula* individuals <2 m in height were measured in four randomly chosen plots per transect. Because many seedlings and saplings were <15 cm in height, the rcd was measured at soil level with a caliper. Tree position was recorded per plot. An individual was classified as 'seedling' if the first, simplified foliage leaf was still attached; all individuals that already had lost their first foliage leaf and were <2 m in height were classified as 'saplings'; individuals >2 m in height and a dbh <19.5 cm were classified as 'juveniles'; all larger individuals were classified as 'adults'. The dbh threshold between juvenile and adult trees was chosen since it was the dbh of the smallest flowering *P. pendula* tree observed within the forest fragment 'Piedade'.

6.4. Results

6.4.1 Germination and seedling establishment

The median total number of *P. pendula* seedlings (Figure 24) underneath the adult tree crowns was significantly higher in the forest edge zone. This higher total number arose from the significantly higher number of newly germinated seedlings in February, approx. one month after pod opening. The number of new seedlings did not differ between the habitats during the remaining year (Table 26).

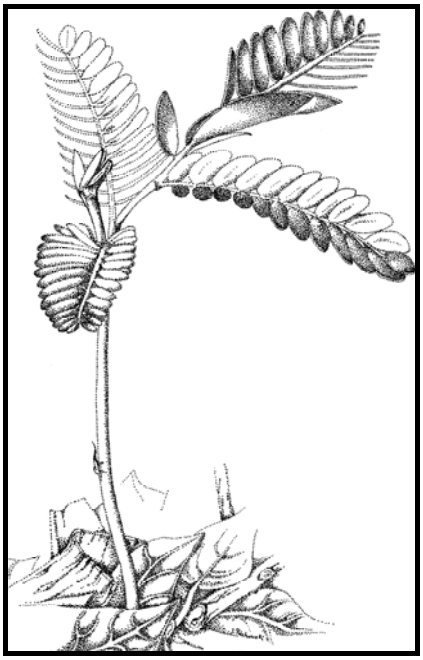

Figure 24 *P. pendula* seedling (Illustration by J. Piechowski after a photograph).

This relation changed dramatically after taking the seed production per tree in the two habitats (Figure 19) into account. In median, 0.21% of the produced seeds germinated underneath the mother trees in the forest edge zone (max: 0.84%). The median germination rate underneath trees in the forest interior was 0.52% (max: 35.42%). This was significantly higher (Mann-Whitney U: 52.0; $p = 0.004$) than in the forest edge zone (Figure 25). The monthly germination rates showed a clear tendency towards a germination of *P. pendula* seeds during the first two months after seedpod opening. Beside this, the ability of a several months lasting germination delay was also obvious, especially in the forest interior (Figure 25).

Table 26 Median number of newly germinated *P. pendula* seedlings per month and 100 m^2 in the forest edge zone and interior.

		n	Median	Min – Max	Mann-Whitney U	p
February	Edge	14	54.9	0 – 417.7	63.5	0.016
	Interior	18	21.2	0 – 283.2		
March	Edge	14	47.8	0 – 60.2	116.0	0.722
	Interior	18	19.5	0 – 166.4		
April	Edge	14	8.9	0 – 31.9	126.0	1.000
	Interior	18	8.9	0 – 38.9		
May	Edge	14	3.5	0 – 49.6	109.0	0.536
	Interior	18	0.0	0 – 17.7		
June	Edge	14	3.5	0 – 31.9	103.5	0.398
	Interior	18	3.5	0 – 10.6		
July	Edge	14	8.9	0 – 31.9	95.0	0.251
	Interior	18	3.5	0 – 46.0		
August	Edge	14	8.9	0 – 38.9	92.5	0.206
	Interior	18	3.5	0 – 46.0		
September	Edge	14	10.6	0 – 35.4	93.0	0.220
	Interior	18	5.3	0 – 60.2		
October	Edge	14	10.6	0 – 28.3	75.5	0.054
	Interior	18	1.8	0 – 31.9		
November	Edge	14	0.0	0 – 10.6	115.0	0.694
	Interior	18	0.0	0 – 7.1		
December	Edge	14	0.0	0	112.0	0.613
	Interior	18	0.0	0 – 3.5		
Total	Edge	14	180.5	0 – 431.9	70.5	0.034
	Interior	18	76.1	0 – 669.1		
	Total	32	154.0	0 – 669.1		

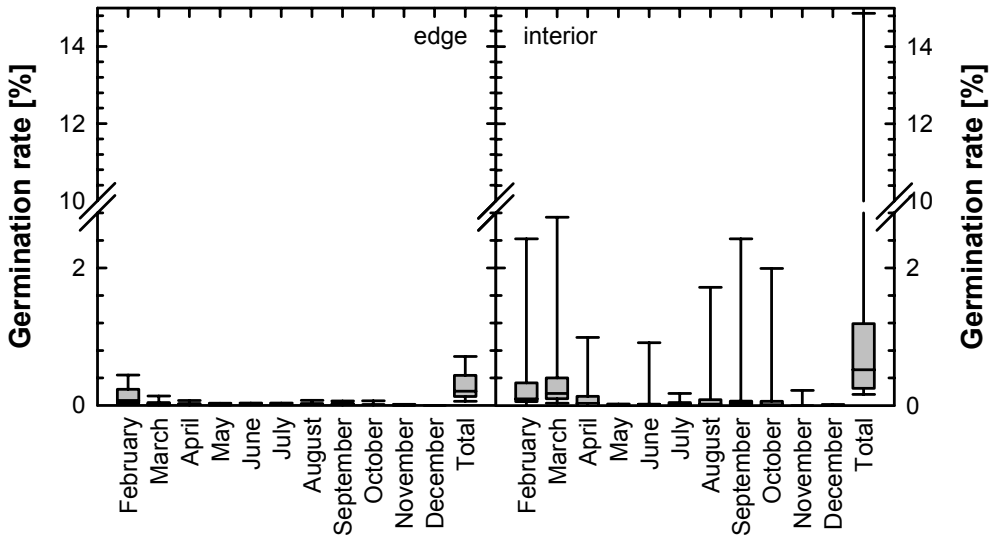

Figure 25 Monthly and total germination rate [%] underneath *P. pendula* trees. Forest edge zone *vs.* interior.

Beside the absolute number of seedlings and the germination rate, the seedlings' median survival time differed also significantly between the two habitats. The median survival time was one month in the forest interior and less than one

month in the forest edge zone (Table 27). The probability to survive the first nine months after germination was three times higher in the forest interior compared with the forest edge zone (13.2% and 4.3%, respectively; Figure 26).

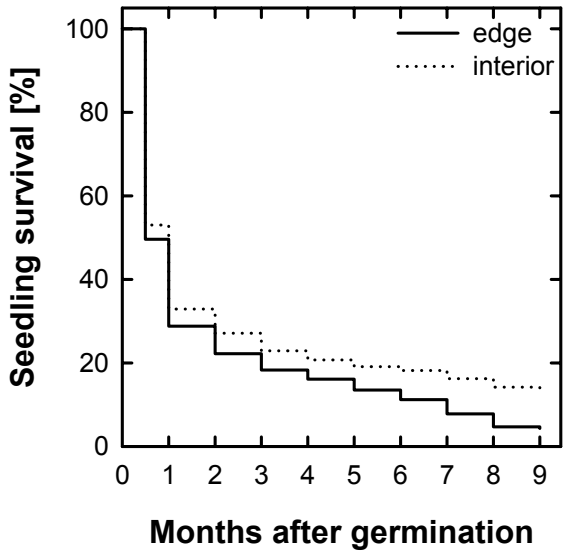

Figure 26 Seedling survival rate [%] underneath *P. pendula* trees. Forest edge zone *vs*. interior.

Table 27 Median survival times of *P. pendula* seedlings underneath the mother trees. Forest edge zone *vs.* interior.

	n	Median [month]	25/75 percentile [month]	Log-Rank statistic	p
Edge	750	<1	2/<1	11.949	<0.001
Interior	715	1	3/<1		

The higher number of germinated seedlings underneath the mother trees in the forest edge zone (Table 26) and the higher germination rate (Figure 25) and higher survival probability in the forest interior (Figure 26) led to an equal seedling density in the two habitats at the end of the observation in December 2004 (Figure 27).

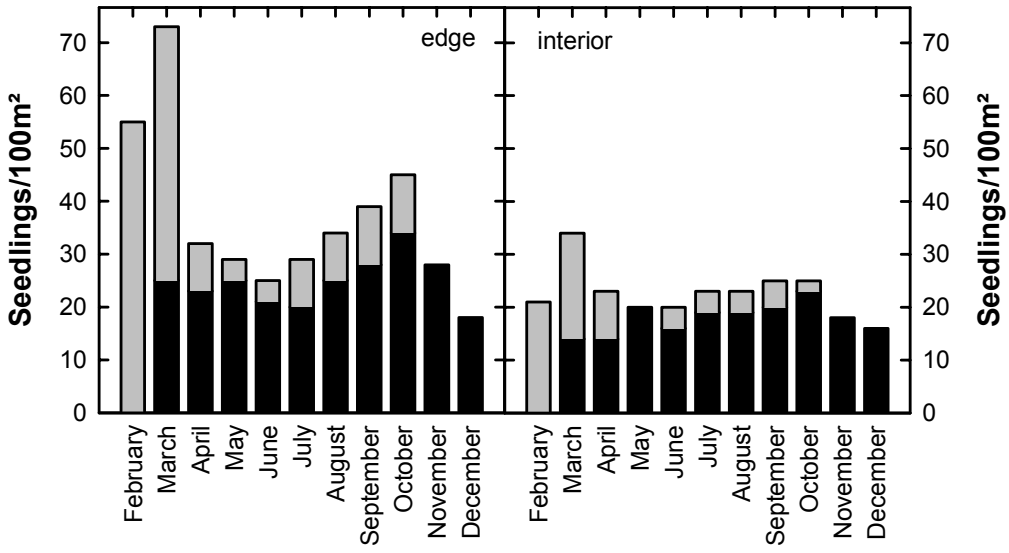

Figure 27 Median number of *P. pendula* seedlings per 100 m². Forest edge zone *vs*. forest interior. Gray bars: newly germinated seedlings; black bars: old seedlings.

The seedlings, which germinated in February and survived until December, 89% had more leaves than just the first, simplified foliage leaf in the forest edge zone and 82% in the forest interior. This was not significantly different (Fisher's exact test: $p = 1.0$).

The median number of foliage leaves differed significantly in March only, when the seedlings in the forest edge zone had 0.07 leaves additional to their first leaf and the seedlings in the forest interior had none (Mann-Whitney U: 63.0; $p = 0.016$). Although not significantly different, there was a trend towards more leaves per seedling in the forest interior later on. In December, the median number of additional leaves was 0.85 in the forest interior and 0.28 in the forest edge zone (Mann-Whitney U: 88.5; $p = 0.156$).

6.4.2 Population structure

Saplings were found to dominate the size-class distribution of *P. pendula* in the forest edge zone as well as in the forest interior, with 335 and 407.5 individuals/ha respectively (Figure 28). Three adult trees/ha were found in the forest edge zone, two in the forest interior (Figure 28). The densities of both size-classes did not differ between the habitats (Table 28).

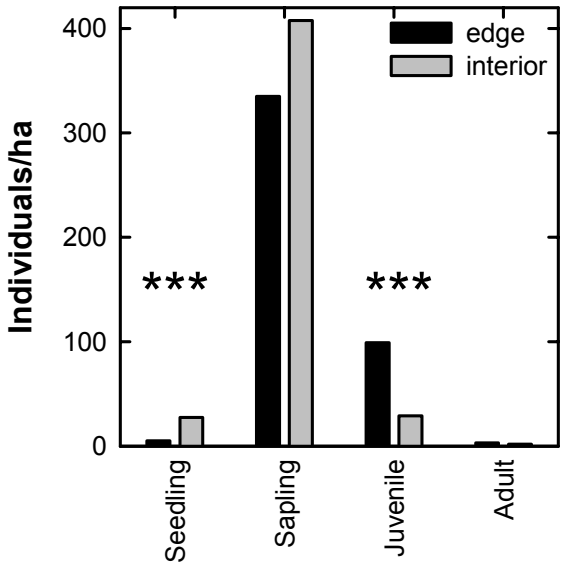

Figure 28 Seedlings, saplings, juvenile, and adult *P. pendula* individuals per hectare in the edge zone and forest interior.

Table 28 Number of seedlings, saplings, juvenile, and adult trees of *P. pendula* per hectare, minimum and maximum per 100 m² plot, and their p-values. Forest interior *vs*. forest edge zone.

		n/ha	Min – Max/ 100 m² plot	Mann-Whitney U	p
Seedling	Edge	5.0	0 – 0.5	3,450.0	< 0.001
	Interior	27.5	0 – 1.3		
	Total	16.3	0 – 1.3		
Sapling	Edge	335	0 – 8.3	4,900.0	0.806
	Interior	407.5	0 – 17.5		
	Total	371.3	0 – 17.5		
Juvenile	Edge	99.0	0 – 10.0	3,626.0	< 0.001
	Interior	29.0	0 – 5.0		
	Total	64.0	0 – 10.0		
Adult	Edge	3.0	0 – 1.0	4,950.0	0.651
	Interior	2.0	0 – 1.0		
	Total	3.0	0 – 1.0		

The densities of the remaining two size-classes differed significantly between the two habitats (Table 28); the seedling density was higher in the forest interior (27.5 *vs*. 5/ha) whereas the density of juvenile trees was higher in the forest edge zone (99/ha *vs*. 29/ha; Figure 28).

Besides differences in densities between the two habitats, the mean diameter and height were also significantly different in two size-classes. Saplings were higher and their rcd was thicker in the forest edge zone (Table 29). Contrary, the fewer juvenile trees in the forest interior (Table 28) were higher and thicker than the juvenile trees in the forest edge zone (Table 29). No differences were detected for these parameters in seedlings between the habitats. The mean parameters for height and dbh were not calculated for the adult tree class due to their low number of individuals.

Table 29 Mean diameter and height of saplings and juvenile *P. pendula* individuals in the forest edge zone and forest interior.

			Mean ± SD	Min – Max	Mann-Whitney U	p
Saplings	RCD [cm]	Edge	0.6 ± 0.5	0.1 – 2.8	8,480.0	0.001
		Interior	0.4 ± 0.5	0.1 – 4.4		
		Total	0.5 ± 0.5	0.1 – 4.4		
	Height [cm]	Edge	37.8 ± 30.3	11 – 171	8,534.0	0.001
		Interior	27.9 ± 20.1	3 – 140		
		Total	32.4 ± 25.6	3 – 171		
Juvenile	DBH [cm]	Edge	4.2 ± 2.9	1.0 – 13.9	1,007.5	0.015
		Interior	6.4 ± 4.5	0.7 – 18.6		
		Total	4.7 ± 3.5	0.7 – 18.6		
	Height [m]	Edge	5.3 ± 2.6	2 – 11	943.5	0.005
		Interior	7.1 ± 3.0	2 – 12		
		Total	5.7 ± 2.8	2 – 12		

6.5. Discussion

6.5.1 Germination and seedling establishment

The calculated germination rates can only hardly be compared with experimentally gained germination rates. The germination rates presented here were computed by the number of seedlings underneath the adult tree crowns divided by the extrapolated number of produced seeds and therefore disregard primary and secondary seed dispersal, on-site predation as well as the problem of germination underneath the mother tree (Janzen 1971). However, primary dispersal of *P. pendula* seeds was rather uncommon in the study area, since only *Callithrix jacchus* acted as primary disperser and its home ranges are small (Scanlon et al. 1989) and most monitored adult *P. pendula* trees were obviously located outside of any of the primate groups ranges. Secondary dispersal of *P. pendula* seeds was very frequent but even the largest dispersing ant, *Pachycondyla crassinoda*, moved the seeds probably seldom

farther than a few meters only (compare seed transport distances of *Pachycondyla harpax* and *P. apicalis* in Horvitz and Schemske 1986), so that they were most likely mainly deposited still within the circular plots. On- site predation rate was the same in both habitats and lowered the calculated germination rate in both habitats equally. Furthermore, density-depending effects (pathogens, predators, parental and sibling competition) are quite unlikely because the seedling density was far below the seedling densities where these effects were proved (Gilbert et al. 2001). Therefore, the here presented rates might be regarded as a rough picture of a more precisely gained experimental germination rate.

The overall calculated germination rate was very low, even lower than the germination rates in the other two studies under field conditions that had approx. 15% (Camargo et al. 2002) and 4.6% (Schulze 2003) in forests. The higher rate by Camargo et al. (2002) might be related to their use of scarified seeds, which has an experimentally shown effect on germination (Barbosa et al. 1984, Scarano and Crawford 1992) although Schulze (2003) did not find any significant difference between scarified and non-scarified seeds under field conditions. Another reason for the lower median germination rate is certainly the way of calculating this rate in the present study excluding all possible interactions with animals and pathogens. Nevertheless, all three studies show quite low germination rates of *P. pendula* in forests compared with laboratory studies (Alencar and Magalhães 1979, Barbosa et al. 1984, Scarano and Crawford 1992) as well as with habitats with higher irradiance, like pasture and bare soil (Camargo et al. 2002). This might be an indication of a germination threshold in light quality (r:fr) or diel temperature fluctuation as it was shown for some Neotropical pioneer species (Pearson et al. 2002, 2003). The significant decrease in germination rate of *P. pendula* in the forest edge zone might be an additional cue for positive photoblastic seeds in this species. The leaf litterfall was significantly higher in the forest edge zone of the studied fragment 'Piedade' (11.01 ± 1.91 *vs.* 8.55 ± 1.46 t ha^{-1} y^{-1}; Schessl et al. in press) and dead leaves on the forest floor decrease the r:fr ratio beneath them and inhibit germination of seeds (Vázques-Yanes et al. 1990, Vázquez-Yanes and Orozco-Segovia 1993). Similar results were obtained by Bruna (1999) who showed that the impact of leaf litter on seed germination is larger near forest edges. This effect could also be the reason for the germination delay of *P. pendula* seeds, which was observed in the recent study as well as in prior ones (Alencar and Magalhães 1979, Schulze 2003).

Beside possible impacts of the highest litterfall values reported for the Atlantic Forest (Schessl et al. in press) on germination rate and germination delay, this higher litterfall might also be a reason for the higher seedling mortality in the edge zone. Personal observations show that a single larger leaf may act as a physical barrier for the delicate seedlings of *P. pendula*, which often led to the seedlings' death.

High seedling mortality due to leaf litterfall was already confirmed experimentally on community level at La Selva (Clark and Clark 1989).

Another factor known to decrease germination rates and increase mortality rates is soil moisture (Bunker and Carson 2005, Gilbert et al. 2001, McLaren and McDonald 2003). Soil (litter) moisture is known to be lower at open forest edges (Didham and Lawton 1999, Kapos et al. 1997). Nevertheless, soil moisture is not suspected to be a major cause for the observed edge effects on germination and survival of *P. pendula* seedlings since the observation year was a very wet one (nearly double the average annual rainfall; Schessl et al. in press). Furthermore, germination rate of *P. pendula* seeds was highest on bare soil and approx. 25% of the seedlings survived the first year at this dry site, whereas germination was much lower in the wetter forest where non of the seedlings survived (Camargo et al. 2002).

6.5.2 Population structure

Several factors might be the reason for the overall very low seedling density. The first obvious reason is the low number of fruiting *P. pendula* trees in 2004/05 in the edge zone and the lack of trees with fruits in the forest interior. All counted seedlings within the transects are therefore most probably 'old' ones from the 2003/04 phase; i.e., they were up to one year old. Therefore, only the small percentage of seedlings that survived the first months after germination were counted. Secondly, many individuals of this 2003/04 cohort may have already lost their first foliar leaf and were therefore included in the sapling group due to the strict group definitions. If all individuals <20 cm – the maximum height of 1 year old *P. pendula* seedlings (pers. observ.) – were classified as seedlings, the densities were 85 and 187.5/ha (edge zone and interior, respectively). However, even with this wider definition, the seedling density was significantly lower in the forest edge zone (Mann-Withney U: 3,550.0; $p < 0.001$). Therefore, the difference in seedling density was not an artifact of class definition. A third important reason for the overall low number of seedlings remote from adult trees is the observation that only few fruiting *P. pendula* trees were visited by the presumed primary seed disperser *Callithrix jacchus*.

The lower seedling density in the forest edge zone can be explained by the processes prior to seedling distribution, which were studied in this survey. The lower germination rate and higher seedling mortality but also higher absolute number of seeds in the edge zone led to an equivalent seedling density underneath the mother trees in both habitats approx. one year after seed release. The recent result of a higher seedling density in the forest interior was recorded three months later (March 2005) and remote from adult trees. This density is most probably the result of the ongoing trend of a higher mortality at the edge and better growth conditions (i.e., more leaves per seedling) in the forest interior. Furthermore, the higher secondary

seed dispersal rate by ants is surely also an important reason for the higher seedling density remote from adult trees in the forest interior. These processes apparently overcompensated for the lower seed production in 2003/04 and even the absence of seeds in the flowering phase 2004/05 in the forest interior.

The distribution patterns of the later size classes (saplings, juveniles, and adults) did not follow the seedling pattern of a higher density in the forest interior. The pattern seems to obvert instead, namely similar densities of saplings and even a higher juvenile tree density in the forest edge zone. Survivorship of the larger size classes was therefore obviously positively affected by the forest edge. Nevertheless, this is somehow contradicted by the taller and thicker juvenile trees in the forest interior. A clear, monotonically edge effect on the population structure of *P. pendula* is therefore not detectable. But these simple effects are "unrealistic to expect" (Murcia 1995) since different effects are likely to interact with each other or processes at one level could obscure or neutralize edge effects at a different level (Murcia 1995). This is especially true, if patterns of long-living and immobile organisms (like trees) are the focus of research with the immense number of possible processes affecting their distribution (establishment I and II in Wang and Smith 2002).

The seedling density therefore is a bad predictor for the patterns of size classes of saplings, juveniles, and adult trees because they were influenced by further factors that were altered by the forest edge. A re-census after a time-span of some years might be the appropriate method to analyze the differences in saplings and juveniles. High-resolution satellite images (< 1 m x 1 m) could enlarge the observation area for the adult size class, since the flat but large crowns of *P. pendula* trees should be easily distinguishable. Furthermore, a re-census will reveal better predictions for the future population structure in the two habitats than the static size class distribution (Condit et al. 1998).

7. Literature

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Appendices

Studied trees

Appendix 1 Dbh, height, and crown area of the studied *P. pendula* adults in the forest interior and the edge zone.

Number	Dbh [cm]	Height [m]	Crown area [m²]
Edge zone			
D007	39.0		89.0
D013	135.3	34.0	804.5
D014	52.5	21.2	90.0
D015	58.3	16.0	169.0
D124	111.4	30.0	261.5
D125	47.3	16.0	142.0
D126	45.7	18.0	87.0
D127	83.9		
D128	57.1		
D129	36.2		
D130	28.4		
D131	47.4		58.0
D132	49.1	17.5	98.0
D133	49.1	20.0	130.0
D134	51.5	21.0	96.0
D135	58.2	19.5	67.5
D136	43.6	17.5	110.0
D137	79.6	21.0	
D181	72.4	17.0	237.0
D812	38.5	17.0	138.5
Interior			
D016	66.1	21.5	188.5
D017	30.3		59.5
D018	37.6	18.5	48.0
D019	37.8	19.5	101.0
D020	34.7	18.0	88.5
D021	52.1	21.5	199.5
D022	106.6	28.0	269.0
D024	49.0		92.0
D025	76.8	22.0	244.5
D026	51.2	25.0	159.0
D117	32.6	16.5	54.0
D118	45.5	19.0	135.0
D120	110.0	22.0	309.0
D121	48.9	22.5	
D122	54.5	19.0	221.0
D123	56.1	20.5	107.0
D161	35.7	21.0	
D162	44.7	19.5	116.5
D163	43.3	15.5	116.0
D164	140.1	28.0	178.0
D165	33.8	21.0	
D166	38.9	20.0	
D167	47.0	18.5	136.0
D180	40.3	19.0	116.5

Photographs

Appendix 2 a: Forest belt, cart track, and sugarcane field at the western side of the forest fragment 'Piedade'; b: *Phyllostomus discolor* with yellow polyads of *P. pendula* at the uropatagium.

Erklärung

Ich versichere hiermit, dass ich die Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie die wörtlich oder inhaltlich übernommenen Stellen als solche kenntlich gemacht habe.

Ferner erkläre ich, dass die von mir vorgelegte Dissertation bisher nicht im In- oder Ausland in dieser oder ähnlicher Form in einem anderen Promotionsverfahren vorgelegt wurde.

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Curriculum Vitae

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03/2003 – present	Scientific assistant, Institute of Systematic Botany and Ecology, Ulm University. Project: Sustainability of remnants of Atlantic rainforest in Pernambuco and its implications for conservation and regional development.
04/2000 – 03/2003	Teaching assistant, Institute of Biology/Zoology, Free University of Berlin. Undergraduate courses in Zoology, Ecology, and Systematics and Evolution.
10/2001 – 12/2001	Field researcher, Chair of Biogeography, University of Bayreuth. Project: Analyses of virgin and disturbed tropical montane forest systems in Southeast Ecuador.
08/2000 – 08/2002	Member of the Students Employee Committee, Free University of Berlin.
10/1999 – 12/1999	Student assistant, Institute of Systematic Botany and Ecology, Ulm University. Project: Analyses of virgin and disturbed tropical montane forest systems in Southeast Ecuador.

05/1998 – 05/1999	Student assistant, Federal Institute for Material Research and Testing, Berlin. Division: Biology in materials protection and environmental issues.
12/1995 – 12/1996	Civil service, Biological Station Gut Ophoven, Leverkusen. Project: Maintenance of biological reserves.
07/1995 – 12/1995	Development aid volunteer, Favela Boa Vista, São Paulo. Project: Constructing of a community center.

Publications

Piechowski D. 2007. Bat visits and changes in floral nectar during anthesis of *Parkia pendula* (Mimosaceae). - Phyton (Horn, Austria) 46: 203-204.

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Schessl M, Gottsberger G, Piechowski D, Krause L. 2007. Brazilian-German research on sustainability in fragments of Atlantic rainforest in NE Brazil: results of the first phase and an outline of future studies. - 20th Annu Meet Soc Trop Ecol, Bonn, Abstracts: 109. (poster)

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Memberships

since 2004	Association for Tropical Biology and Conservation (ATBC)
since 2004	International Canopy Network (ICAN)
since 1999	Society for Tropical Ecology (gtö)