Living under water for up to four months of the year: observations on the rheophytes of the Mekong River in the Pha Taem National Park area (Thailand/Laos border)

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ABSTRACT. Rheophytes of the Mekong were investigated in the Pha Taem National Park area (Thailand/Laos border); a stretch of river ca. 100 km long was studied. The unusually harsh environmental conditions (water levels changing by several meters; plants submerged for up to four months per year) are described, and general characteristics and adaptations of these "extreme rheophytes" are elaborated on. The kinds of rheophyte habitats are characterized. A list of observed rheophytes (25 taxa) is provided and comments are made on their distribution patterns both in the study area and elsewhere. A comparison with "Siphandone Wetlands", a well studied area of the Mekong in southern Laos, is included.

KEY WORDS: Mekong, rheophytes; Pha Taem National Park, Thailand/Laos border.

INTRODUCTION

The Mekong is the 12th longest river in the world (4,800 kilometers), the longest in Southeast Asia and the only international river in Asia to cross six countries. It originates on the Tibetan Plateau, at an elevation of about 5,000 meters, flows southwards passing through China, Burma (Myanmar), and enters its lower basin at the common Burma-Laos-Thailand boundary point boundary point (Chiang Rai Province of Thailand). From there, the river flows eastward and enters Laos; North of Luang Prabang it turns southward again to rejoin the Thailand – Laos border around Chiang Khan (Loei Province). From this point, the Mekong, over a stretch of almost 700 km, marks the Thailand – Laos border (from Loei to Ubon Ratchathani Province) before continuing through southern Laos to Cambodia, Viet Nam and, finally, the South China Sea. In terms of average discharge (15,000 cubic meters of water per second) it ranks as 8th largest river on a worldwide scale. Discharge (and, subsequently, water level), however, is highly seasonal, and about 80% of its discharge occurs between June and November (see Fig. 1); in September, 20–30% of the total annual flow travels down the Mekong. The reasons for this seasonality are many-fold, but the primary reason is that in the entire Mekong river basin about 85–90% of the annual rain falls between May and October, during the southwestern monsoon. Also the summer snowmelt in eastern Tibet contributes considerably to the Mekong's high discharge during the second half of this period. Superimposed on this general pattern are irregularly occurring large floods (e.g. in August 1998, September 2000, or the latest in August 2008). – Information contained in this paragraph originates mainly from the following sources: Douglas (2005), Gupta et al. (2002), Gupta & Liew (2007), Hiroshi (2000), Hoanh et al. (2003) and various publications of the Mekong River Commission (MRC) available on the internet (MCR undated, MRC 1997, MCR 2008).

From the above follows that, in parts of the study area (see below for details), the water level of the Mekong in the rainy season (June–November) is several – locally probably up c. 6–8 – meters

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higher than in the dry season (December–May) (Fig. 2). The mean monthly discharge data from Mukdahan gauging station, North of the study area, corroborate this (Fig. 1). Thus, plant life (predominantly trees and shrubs) in at and the immediate edge of the Mekong exists under extreme conditions: During periods of the highest water levels they are entirely submerged and "invisible." In the study area they are typically living underwater up to 4 months, in the time frame June to November (annual fluctuations, depending on the rainfalls in the Mekong basin are possible); elsewhere on the Mekong, this period may be extended to up to 6 months (see Discussion). Only when the water level goes down again, their presence (and richness!) becomes apparent, and in the dry season they are often living in seemingly bone-dry habitats such as cracks of rock or sandbars or sandy shores (see Rheophyte habitats, below). These plants are rheophytes of a rather extreme kind, apparently under much more strain than "typical" ones elsewhere. Normally, rheophytes will hardly ever be submerged for such a long period of time (short or long heavy tropical rainstorms in the upper reaches of a stream may cause the water level to rise for several hours to a few days, or – during a longer rainy spell – for a few weeks, but not usually for several months). The aim of this paper is to draw attention to rheophytes and their characteristics and adaptations in general, and to the under collected, ill documented and fascinating rheophytes of the Mekong in particular, and to encourage further studies (as the present one is limited to a relatively short stretch of river).

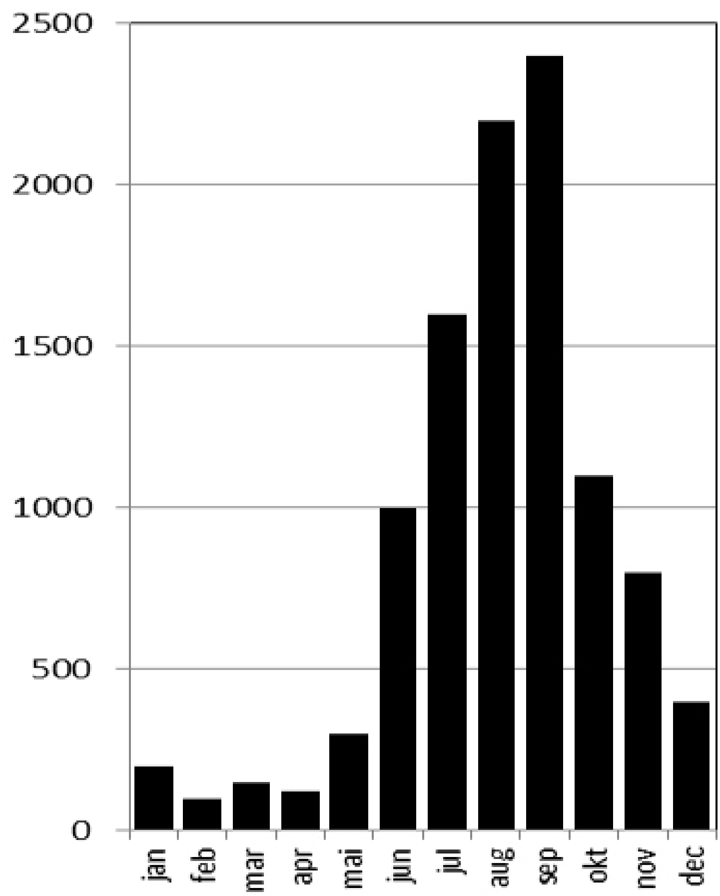

Figure 1. Mekong mean monthly discharges at Mukdahan gauging station in cubic meters per second (excerpted and redrawn from Douglas 2005, fig. 12.4).

Figure 2. Mekong river in A, the dry and B, wet season (from Pha Mon viewpoint, Pha Taem National Park; a conspicuous Ficus tree on the river shore marked as reference point; the hills on the opposite side of the river are in Laos). The rocky areas with their rheophyte populations (the latter particularly conspicuous on the far side of the river!) are no longer visible (i.e., fully submerged) in B. A, Feb. 20, 2008, photograph C. Puff; B, August, 30, 2008, photograph Pha Taem National Park staff).

RHEOPHYTES AND THEIR CHARACTERISTICS

By definition (van Steenis 1981, 1987) rheophytes are plant species which are in nature confined to the beds of swift-running streams and rivers and grow there up to flood-level, but not beyond the reach of regularly occurring flash floods. There are basically 2 types of rheophytes – obligate rheophytes (to which the above definition applies in the strict sense) and facultative rheophytes (plants possessing a wide ecological tolerance, able to exist both in "typical" rheophyte habitats and elsewhere).

The bulk of Mekong rheophytes belong to van Steenis' (l.c.) life-form group of "rheophytic land plants" (mostly shrubs, some small trees but also a few perennial herbs). The other categories distinguished by him, "hydrophytic rheophytes" (permanently submerged herbs) and "torrenticolous rheophytes" (herbs submerged in vegetative state and flowering periodi¬cally when waters are low), are poorly represented in the study area (for a possible explanation see below for details).

Following van Steenis (l.c.), rheophytes are good example for a "biological group" of organisms, in that they share a restricted ecological environment without being related systematically, i.e. recruited from diverse families (other examples of biological or ecological groups would be mangroves, lithophytes or epiphytes).

Adaptive features/characteristics of rheophytes

Life and survival in or at the edge of a river puts extreme – and very diverse – strain of the plants growing there: (1) at times of high floods, the submerged plants must be able to resist the power of the flowing water. (2) when the water level is low and plants are exposed, growing on hot, dry, exposed rocky, gravelly or sandy areas, they must be able to survive the months-long dry period. In adaption to these conditions, rheophytes tend to show the following adaptations:

– Seedlings soon develop an extensive root system (much more extensive than the above ground parts), securely anchoring the plant in the substrate, so that during the next high water period it is not washed away (seeds germinate in the dry season).

– Shoots tend to be tough and flexible (i.e. they do not break easily) and the often simple leaves are frequently narrow, short-petioled and flexible; that way the resistance to the fast-flowing water during floods will be minimized. There are exceptions to these adaptations, compensated by others: Stiff-stemmed shrubs depend mainly on firm anchorage, i.e. an extraordinarily strong root system; in plants with compound leaves, leaflets tend to be narrow and flexible.

– Extensive root systems are an adaptation to overcome the dry period. They not only firmly anchor a plant during spates but also guarantee an adequate water supply.

– Diaspore dispersal: With regard to (local) fruit and seed dispersal of rheophytes, water is expected to play a major role. In several rheophytes, buoyant seeds have been observed, but in many others the seeds are sinkers (not a disadvantage as they will germinate only after the water level is low). Others are known to have floating indehiscent fruits. Since rheophytes are recruited from many diverse plant families, it is not surprising, however, that dispersal units of many taxa show no obvious adaptation at all. It is, however, likely that many of the latter are eaten (dispersed) by fish (see Table 1). In general, little detailed information is available of the dispersal mode of rheophyte fruits and seeds. Some observations relevant to taxa in the study area are included in the List of observed rheophytic taxa (below).

See also Lytle & Poff (2004: table 1) for a comprehensive summary of adaptations to flooding and drought, and their costs and benefits.

From the above characterization it follows that rheophytes are part of the riverine vegetation, but riverine plants are not necessarily rheophytes, i.e. not all plants occurring along the Mekong are rheophytes. For example, any woody plants growing above the (typical) high water mark are certainly not (in times of exceptional floods, their stems may, however, be basally submerged for some time). As the low water/dry period is long, various herbaceous plants can germinate and settle in “rheophyte habitats.” If annual, they will be able to flower and fruit within the low water period. If perennial, they may not be able to reproduce before the next high water/wet season. In any case, the vast majority of these will be washed away when the river is high. An example from the study areas is the weedy Paederia linearis (Rubiaceae) which occasionally occurs in depressions of Mekong “rock islands” but is much more common in disturbed areas above the high water level. Another is *Ricinus communis* (Euphorbiaceae) which may form rather large populations in nutrient rich depressions of the river bed, probably coming into flower within months after germination; these populations will, without doubt, not survive the next flooding periods. None of these types of annual or perennial plants can be classified as obligate or facultative rheophytes and are, therefore excluded from the present study.

Table 1. List of rheophyte dispersal units found in stomachs of fish (*Pangasius* spp.) [taxon name preceded by #] and reported as being regularly eaten by fish [taxon name preceded by §] in Khong Dist., Champasak Prov., Laos. Compiled from Braid (2007). Taxa also found in the study area are marked with an asterisk and will be dealt with in the List of observed rheophytic taxa.

§ *Acacia harmandiana**	§ *Morinda talmyi* (as “*tamyi*”); probably confused with the similar *Morinda pandurifolia**
# *Crateva magna**	§ *Morindopsis capillaris* *
# *Ficus heterophylla**	# *Syzygium mekongense* (as “*Eugenia mekongensis*”)*
§, # *Mimosa pigra**	# *Telectadium edule* H. Baill. (Asclepiadaceae)

STUDY AREA

Starting from around the Mekong – Mun (Moon) River confluence northwards, a stretch of the Mekong River, roughly 100 km long, was investigated in detail (see Fig. 3A). Most of this river portion is formally part of Pha Taem National Park (PTNP). Outside PTNP is only a c. 2 km long stretch North of the confluence of the two rivers. The areas South and West of the Mekong – Mun confluence are part of Kaeng Tana National Park. In addition, "spot checks" of the Mekong River rheophytic vegetation were made in various other places North of the actual study area (notably in Amnat Charoen and Mukdahan Provinces).

The study area was visited four times between 1997 and 2010, in February, May, June and December, i.e., primarily in times with a relatively low water level, when rheophytes were not (wholly) submerged.

Rheophytes were studied either by approaching the Mekong from the land, or by boat (provided by PTNP), which made it possible to visit "rock islands" and shore areas not easily reached by land as vast parts of PTNP are undisturbed and largely uninhabited wilderness without any roads and tracks.

Because many rheophytes of different taxonomic alliances are habitually similar and plants are, therefore, difficult to distinguish from a distance, it was generally considered to be not good enough to observe and identify them from the boat (with or without binoculars) but to explore as many rheophyte areas as possible on foot. Vouchers of rheophytic taxa were made by Mr. Montri Tanaros and are deposited under his collection numbers in herbarium BKF.

In the study area, Mekong mid-river is the international boundary between Thailand and Laos and some of the Mekong River islands formally belong to Laos. Therefore, some of the observations do not strictly refer to Thailand territory. Moreover, in some cases, plants from the Lao shore were studied on foot or from the boat with the naked eye or using binoculars.

Geology and geomorphological features of the study area

The geology of the study area is known only in broad outline (UN-ESCAP 1990). In the study area, the Mekong cuts through the Khorat Plateau which, geologically, extends eastward into western Laos and consists of postrift Jurassic – Cretaceous sedimentary rock (continental). The river appears to follow regional structural trends for most of its course, a pattern interrupted by short reaches with rapids where it deviates from the regional trend (Gupta et al. 2002). Downstream from the study area, the river turns eastwards into Laos and then southwards, where it flows in a rocky course with rapids interspersed with alluvial reaches; still further south, immediately North of the Laos – Cambodia border, the river enters the famous "Sipandone Wetlands" area (Daconto 2001, Brambati & Carulli 2001).

Consequently, the Mekong river bed and the river shores are varied in the study area: steep banks without rocks, steep rocky banks, moderately steep, sandy river banks, rocky rapids, small to large "rock islands" or rocky-sandy islands, sand banks in the river, etc. Below is a summary, with emphasis of rheophyte habitats.

Rheophyte habitats and local rheophyte distribution in the study area

(i) Rocky areas (Fig. 3B–F, 4)

Numerous large sheet-like rock areas which are exposed during low water periods characterize the study area (Fig. 3B, D, F). Sometimes they form "rock islands" (Fig. 3C). In places, there are table-like rock shelves through which the Mekong passes (Fig 3E). In other areas, piles of large boulders are present, while elsewhere rocks may be rather broken up in small, often obliquely arranged rock sheets. Arrangement and structure of the rocks have some influence on the rheophyte populations (see below).

Rocky places are undoubtedly those areas with most – and with the highest diversity of – rheophytes. Yet, there are differences: large, +/- uniform horizontal rock shelves with few boulders are relatively sparsely populated (because they, in general, have few cracks between which woody plants can anchor themselves with their roots); such "micro habitats" tend to be characterized by a specific set of rheophytes. The usually relatively large rocky areas with an irregular and varied topography, on the other hand, generally have the highest plant density and diversity. In terms of diversity, rocky areas consisting of piles of large boulders, or rock slabs piled on top of each other, tend to be intermediate.

Water pools of varying sizes and depths are not uncommon in depressions of sheet-like rock areas (Fig. 4B). Shallow pools will dry up within a few weeks after the Mekong water level has gone down. Deep pools will stay wet for most of the dry season; around their edges various newly established short-lived sedges (Cyperaceae) are occasionally seen (strictly, these are not rheophytes but plants which have grown from seed after the Mekong has retreated; presumably they will perish when their microhabitats are flooded again in the following rainy period).

Rather flat and even rocky areas are, in places, densely covered by a thick layer of muddy sediment; as the dry season proceeds, this will break up into irregularly shaped “mud bricks” (Fig. 4C). This layer is bound to be extremely rich in nutrients (fertilizer washed down the river!); it is quite likely that they are of benefit to rheophytes occurring in such areas [locals do collect these “mud bricks” and mix them with the natural soil of their home gardens!].

(ii) Sandy areas (Fig. 5A–B)

As compared to rocky areas, sandy places are much more uncommon, although occasionally locally very extensive. They are mainly present along the river banks, forming relatively flat to moderately steep slopes (Fig. 5A).

Under certain conditions, sand brought down the river accumulates and forms small “sand hill islands,” sometimes several 100 square meters in extent and over 10 meters high. Sand can also collect in depressions of rock sheets, forming small to moderately sized “sand fields” or pockets (such areas will then have a mixture of sand- and rock-loving rheophytes).

Sandy banks, in various places, are used by the locals for the cultivation of maize or, more commonly, various vegetables, notably beans (and indication that there must be enough moisture and nutrients). These cultivations do not appear to have a serious negative effect on the native rheophytes, as the domesticated plants are planted around them (note beans cultivated in horizontal rows in Fig. 5A–B); nowhere was it seen that rheophytes had been removed.

The set of “sand rheophytes” differs quite strikingly from rheophytes found in rocky areas. Apart from the omnipresent Homonoia riparia, they tend to be different taxa. “Sand rheophytes,” moreover, tend to differ in habit: They are often forming large clumps or “giant cushions” (Fig. 5A–B). As compared to rocky rheophyte habitats, sandy areas have a rather limited rheophyte diversity.

(iii) Other rheophyte habitats

On certain stretches of the river, the banks are steep to very steep and loamy or sandy-loamy, or the river is bordered by +/- vertical rock, while “rock islands” and/or sandbanks are entirely missing (Fig. 5C–D and 14A, respectively). In general, these areas appear to be rather unfavorable for the establishment of rheophytes. They are sometimes almost completely absent or restricted to few taxa (or a single species – e.g. Ficus heterophylla, Fig. 14A). Rheophyte frequency and diversity, however, increases again if a few large rocks or boulders or isolated rocky outcrops are present on these steep banks (Fig. 5D).

It is common to see vegetables planted in terraces on these steep, loamy banks (especially around Khong Chiam town, North of the Mekong – Mun R. confluence; outside PTNP). Obviously the soil on the banks is rich in nutrients (fertilizer washed down the river) so that plants grow well and fast and can be harvested before the next flooding period (during which these areas will be submerged).

Local rheophyte distribution and distribution patterns in the study area

Distribution of rheophytes along the stretch of river investigated is invariably discontinuous (some times more sometimes less so), because it is closely linked to the presence of suitable habitats. This even applies to common, ubiquitous rheophytes with unspecific habitat requirements such as Homonoia riparia, which is conspicuously absent from areas with steep, loamy river banks (where it apparently cannot establish itself) (see map, Fig. 6C).

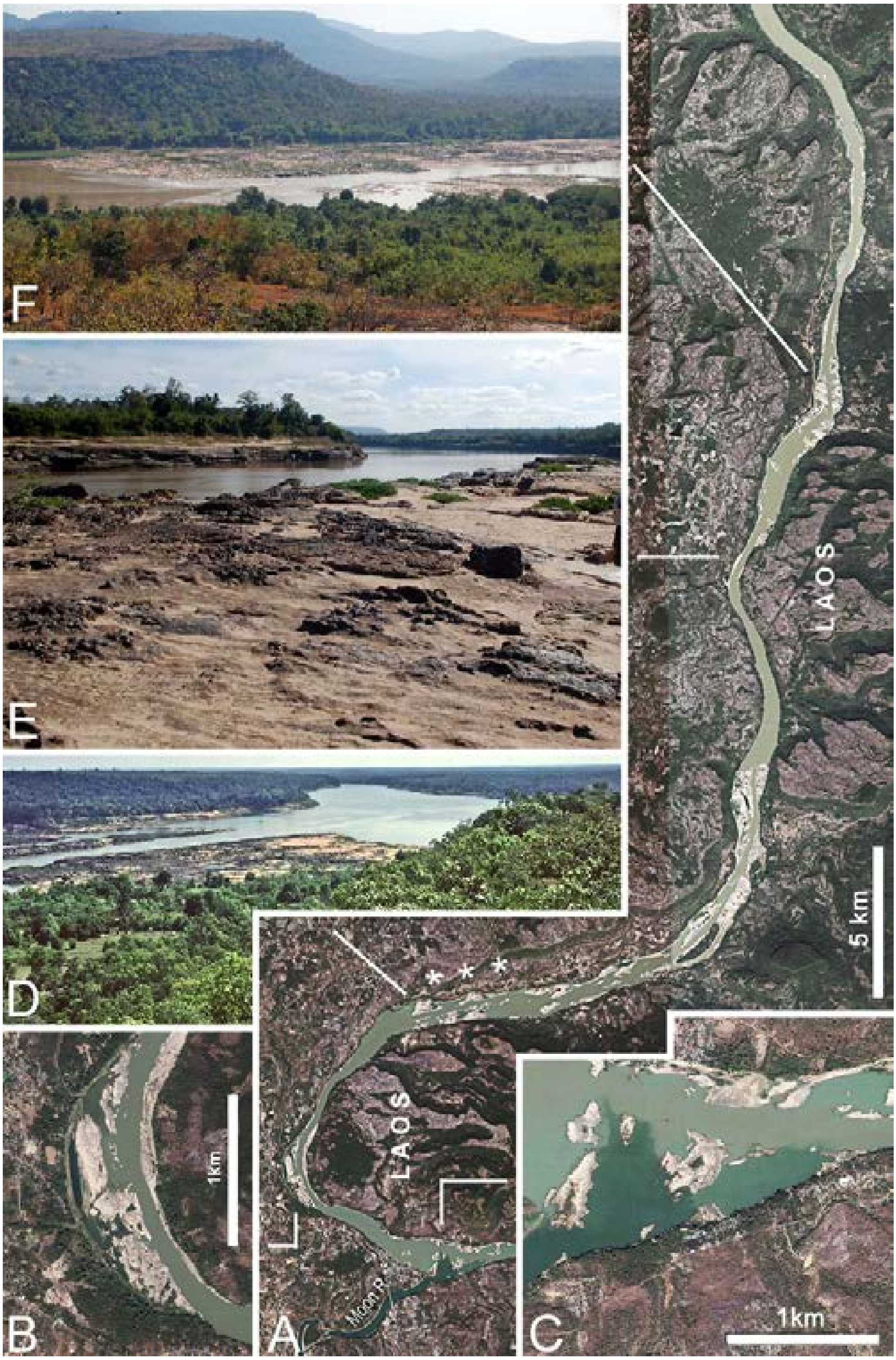

Figure 3. A. Dry season satellite image of the study area, roughly from the Mekong – Moon River confluence northwards; mid-Mekong forms the border between Thailand and Laos (to the East); rheophyte-inhabited rocky and sandy areas clearly show up (see magnified views B and C); *** indicates the core part of Pha Taem National Park; D–F. views of areas indicated in A. Photographs (D–F) C. Puff.

Figure 4. Habitats, part 1. A, extensive broken rocky area in the river bend North of the Moon River junction (see Fig. 3B; *Syzygium mekongense* in the foreground). B, large +/- flat-rocked area near Khum village (see Fig. 3D), shallow to quite deep depressions form pools which do not dry up entirely in the dry season (*Syzygium thorelii*, and some *Homonoia riparia* plants recognizable); the rock sheets are covered by a thick layer of sediments which start cracking during the hot dry season (see C). D, "rock shelf" whose flat top is several meters above the water level in the dry season. E, view from the top of such a "rock shelf" (*Morindopsis capillaris* in the foreground). All photographs C. Puff.

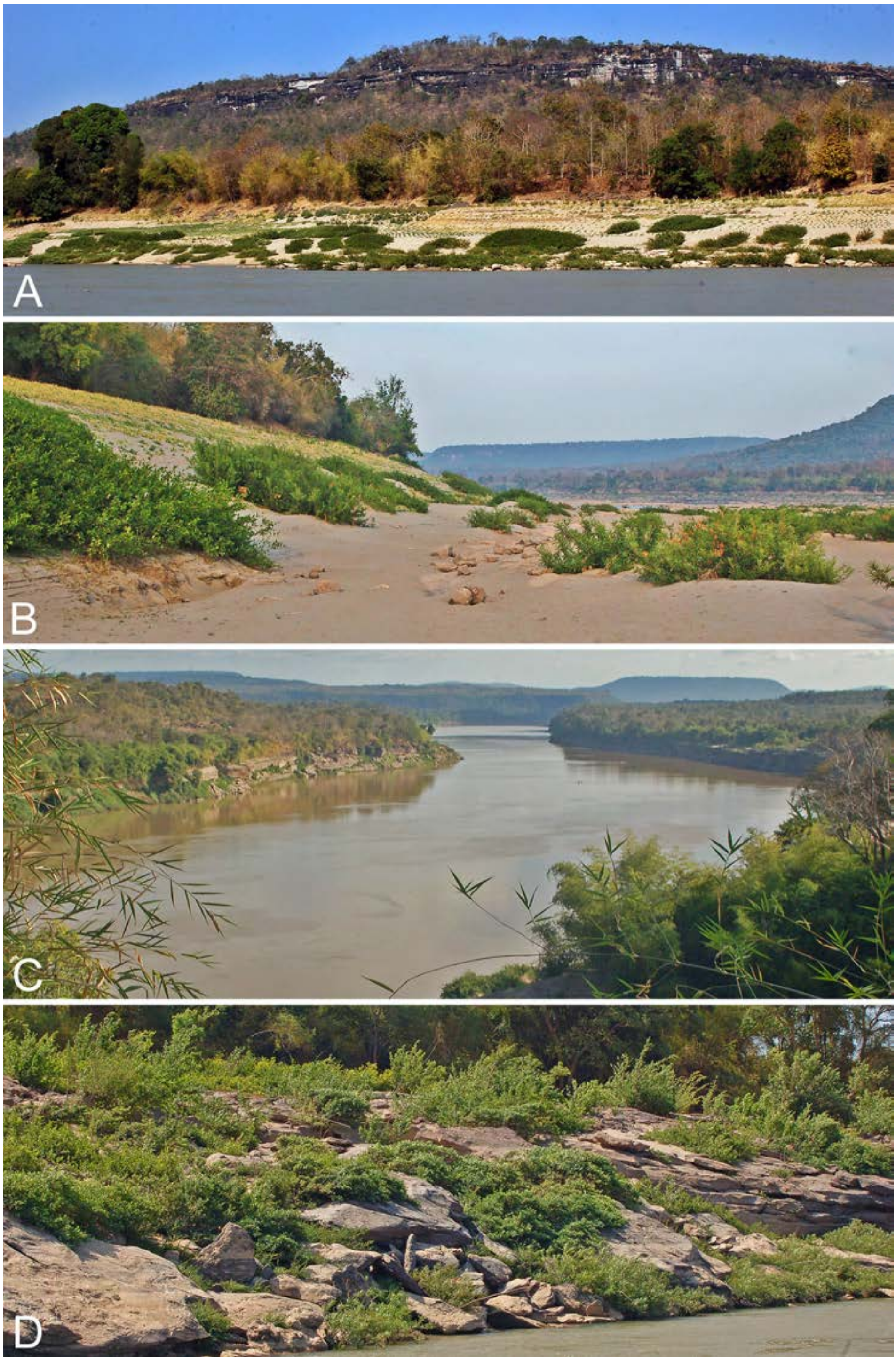

Figure 5. Habitats, part 2. A–B. Sandy river bank and sandy area along the river shore, A from the boat and B the same area from the land (the "giant cushions" on the river bank are *Combretum trifoliatum*, above them bean plantations; also *Homonoia riparia* is recognizable). C. Area of the river with relatively few rheophytes (on steep rocky bank, in the distance left; detail with more rheophytes: D). All photographs C. Puff.

Specific "sand-rheophytes" such as *Combretum trifoliatum* (Fig. 5A–B) will automatically have a discontinuous distribution because sandy habitats are scattered and sometimes several kilometers apart. Although rocky areas are much more common, the same also holds true for "rock rheophytes."

Distribution patterns.

During the field work, it soon became very obvious that individual rheophytic taxa, independent of their habitat preferences, showed markedly different distribution patterns and striking differences in population sizes.

(1) **Common:** ubiquitous rheophytes with a relatively (but not completely) continous distribution and unspecific habitat requirements; usually occurring in large populations (e.g. *Homonoia riparia*, both in rocky and sandy areas; see map, Fig. 6C).

(2) **Scattered:** rheophytes with a rather scattered distribution (populations a few to several kilometers apart), either (a) with unspecific habitat requirements (i.e. rocky AND sandy areas; e.g. *Salix tetrasperma*) or confined to (b) rocky OR (c) sandy habitats (e.g. *Morinda pandurifolia* or *Combretum trifoliatum*, respectively); individual populations small to relatively large.

(3) **Rare:** rheophytes with a very fragmented distribution (populations often many kilometers apart), either growing in (a) rocky OR sandy habitats (e.g. *Artabotrys spinosus*; map, Fig. 6B) or (b) strictly restricted to rocky areas (e.g. *Anogeissus rivularis* or *Morindopsis capillaris*; maps Fig. 6A–B); individual populations very small to medium-sized.

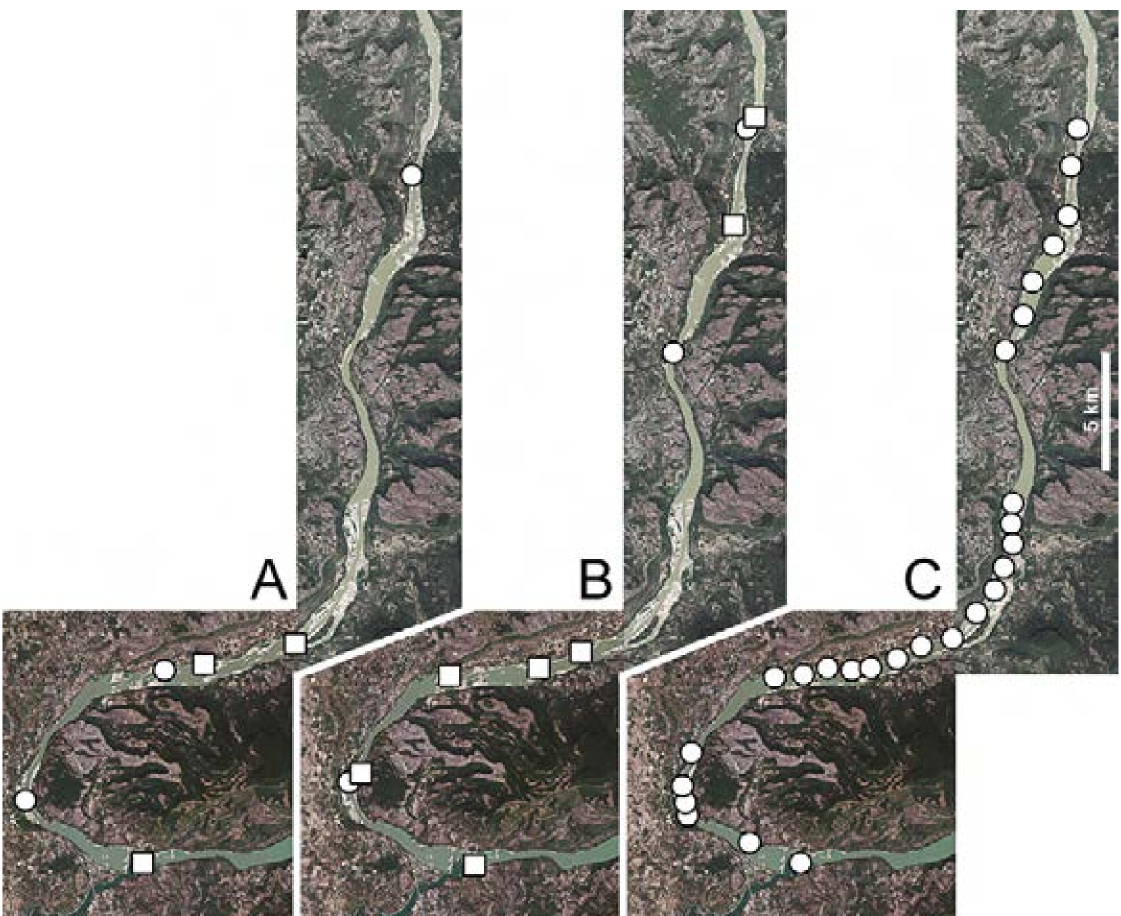

Figure 6. Distribution of selected rheophytes in the study area. A. *Acacia harmandiana* (dots) and *Anogeissus rivularis* (squares). B. *Morindopsis capillaris* (dots) and *Artabotrys spinosus* (squares). C. *Homonoia riparia*.

Phenology of rheophytes in the study area

Flowering and fruiting of rheophyte trees and shrubs is obviously limited to periods of low water level. The first trees and shrubs start flowering as soon as the water level starts dropping. A fair amount of flowering was observed in December, but flowering seemed to be at its peak in February (*Syzygium mekongensis* and *S. thorelii*, *Acacia harmandiana*, *Morinda panduarifolia*, *Homomoia riparia*, etc.). At this time, early flowering taxa such as *Anogeissus rivularis* or *Gymnosporia mekongensis* were already developing fruits. All rheophytes thus complete their reproductive cycle in the dry/low water period.

Many of the rheophytic trees and shrubs are deciduous. New foliage is produced when the water recedes, i.e. normally in November/ December, after the main floods. It was noted, however, that rapid growth of new leaves can also take place "off-season," namely following a small and short-time flood. Fig. 7 (photographs taken in June, i.e. before the "big floods") documents this well: No longer submerged individuals of *Syzygium mekongense* have already started to develop new leaves (Fig. 7C–D), while those growing in slightly lower habitats (below the flood mark – arrow in Fig. 7B; longer submerged than those in Fig. 7C–D) are only about to drop their leaves. Assuming that the water level stays low, these will soon start producing new foliage as well, shortly after dropping the dead ones.

The observation that the leaves of most deciduous trees and shrubs are shed underwater during flooding periods has also been reported for the "swamp forests" of Tonle Sap (Cambodia) which are "flooded by a maximum of 4–6 m of water up to 8 months per year" (Campbell et al. 2006). They, moreover, also pointed out that that certain taxa deviate from this pattern in that they keep their actively photosynthesizing leaves even when submerged for several months; they specifically mentioned *Barringtonia acutangula* and *Combretum trifoliatum*, two taxa which are also recorded from the study area.

OBSERVATIONS

List of observed rheophytic taxa

Arranged alphabetically by family* and genus [* family names and circumscriptions according to Flora of Thailand].

Notes on ecology and distribution patterns are strictly based on observations in the study area, unless stated otherwise. So are, if applicable, the short diagnoses (which, therefore, may deviate from "general" flora descriptions).

The list also includes *facultative* rheophytes (taxa with a wide ecological amplitude also found in non-rheophytic habitats) and some woody "oddities" which hardly deserve to be called *facultative* rheophytes; they nevertheless seem survive together with "typical" rheophytes – see the "Comments" paragraphs of the taxa in question!

ACANTHACEAE

Hygrophila incana Nees (Fig. 12C–D)

Clump-forming perennial herb, stems ascending to erect. Leaves subsessile, opposite, linear(-lanceolate), margins wavy. Flowers 5-merous, several in axillary clusters, subtended by leafy bracts and linear bracteoles. Calyx 5-lobed. Corolla pale violet with darker veins, 2-lipped, lower lip 3-lobed, upper lip shallowly dentate at apex. Stamens 4, hidden below upper lip. Ovary with filiform style and indistinctly 2-lobed stigmas, barely exserted from corolla. Fruit capsular, linear-ellipsoid to narrowly oblong, several-seeded. Seeds compressed, with appressed hygroscopic hairs.

Ecology and distribution pattern (DP): Exclusively found in rocky areas covered by thick mud layers, growing in cracks of rocks; populations small (less than 10 individuals). – DP: "rare"; only seen in two places.

Dispersal: No detailed information available on special adaptations of the seeds.

ANNONACEAE

Artabotrys spinosus Craib (Fig. 8A–D)

Multi-stemmed shrubs, often low and rounded in rocky habitats and taller, less branched (branches often ascending-erect) in sandy areas; some shoots with short, straight spines. Flowers bisexual, 3-merous, solitary; thick and hooked peduncles (as common in other Artabotrys spp.) absent. Sepals 3, small; petals 3+3, several times larger than sepals.

Stamens and carpels numerous, free. Fruits comprised of several to many free, indehiscent, sessile "monocarps."

Ecology and distribution pattern (DP): Found both in rocky and sandy habitats, but less frequent in the latter; populations appear to be never overly large but usually consist of several to c. 20 +/- scattered individuals. – DP: "rare"; populations of well separated from each other (see map, Fig. 6B).

Dispersal: Detailed information unavailable, but presumably the individual mature carpels (monocarps) are capable of floating.

CAPPARACEAE

Crateva magna (Lour.) DC. (Fig. 8E)

For description and illustrations of flowers and fruits see Puff & Chayamarit (2006: 50–51 and 2007: 56–57).

Ecology and distribution pattern (DP): Associated with rocky areas; individuals solitary or in populations of rather few. – DP: "rare"; only few populations, several kilometers apart, were observed.

Dispersal: Presumably, the indehiscent berry-like fruits float at first (their thick, leathery skin probably assures that the seeds, embedded in a soft pulp, stay viable for a longer period of time). Eventually, they are likely to disintegrate, releasing the seeds. In Laos, the latter have been found in fish stomachs (see Table 1 for details and reference).

Comments: An example of a taxon, where the rheophyte status is sometimes only obvious in juvenile state (as seen in fig. 8E). Once fully grown into trees with distinct trunks, the crown (or most of it) may not be submerged during high water periods (the leaflets of the trifoliate leaves, nevertheless, have the "streamlined" shape typical of rheophytes both in juvenile and adult stage). – Various other taxa show a comparable behavior (i.e. they are "typical" rheophytes in juvenile state only): e.g. various Rubiaceae, namely *Nauclea orientalis* (not seen in the study area but nearby, along the Mun river, c. 1 km upstream from its confluence with the Mekong; Kaeng Tana National Park), or the allied (African) *Breonadia salicina* (syn., inter alia, *Nauclea salicina*) (Puff 2003).

CELASTRACEAE

Gymnosporia mekongensis Pierre ["*Maytenus mekongensis* Ding Hou" – see comments] (Fig. 11A–D)

Description based on plants in the study area: small monoecious shrubs with axillary and/or terminal spines (short lateral branches ends in a spine); leaves clustered on short shoots. Inflorescences fasciculate or solitary, axillary or crowded at upper part of a short-shoot, inflorescences axes red. Flowers (greenish-)white, 5-merous unisexual, with a conspicuous fleshy, cup-like nectar-producing disc. Stamens half as long as the oblong-elliptic petals (in male flowers; reduced to considerably smaller staminodes in female flowers). Ovary 2- (seldom 3-)locular, style with 2(3) stigmas (in female flowers; all female parts much reduced and sterile but recognizable in male flowers). Fruit an obovoid capsule; seeds with a small aril attached at the base. – Complete description (partly deviating) in Ding Hou et al. (2010).

Ecology and distribution pattern (DP): Mostly found in rocky areas ("rock islands"), typically in populations of a few to several (to many) individuals; normally associated with *Acacia harmandiana* populations. – DP: "rare"; only few populations, several kilometers apart, were observed.

Dispersal: The arillate seeds indicate ornithochory as primary dispersal mode. Tests with freshly collected seeds, however, showed that they are able to float in water (although it is not known how long before they start to sink).

Comments: (1) In "Thai Plant Names" (The Forest Herbarium 2001) and Newman et al. (2007), this taxon is called "*Maytenus mekongensis* Ding Hou" and in Maxwell (2001) "*Gymnosporia* (*Maytenus mekongensis* Pierre)". There is no reference to this name in the Celastraceae treatment for Flora of Thailand (Ding Hou et al. 2010), presumably because it may have been a nomen nudum, established before arguments have been brought forward that *Gymnosporia* should be considered a genus distinct from *Maytenus* (see, for example, Jordaan & van Wyk 2003).

(2) In the populations seen individual plants were always monoecious (i.e., had both male and female flowers) but polygamodioecy and dioecy

are also known to occur in the species.

(3) A facultative rheophyte, also known to occur in various other habitats.

COMBRETACEAE

Anogeissus rivularis (Gagnep.) O.Lecompte (syn. *Finetia rivularis* Gagnep.) (Fig. 9)

Trees to c. 10 m tall; leaves opposite or subopposite. Flowers 5-merous, in axillary or terminal pedunculate heads. Sepals connate into a stalk-like tube below and expanded into a 5-lobed campanulate cup above. Petals absent. Stamens 5+5. Ovary inferior, uniloculate. Fruits indehiscent, numerous, small, packed into dense cone-like heads (but fruits not fused with each other); individual fruits 4-ribbed, with the persistent calyx-stalk forming a beak (breaking near the middle), appearing asymmetrical as the 2 lateral ribs are stronger developed than the dorsal ones [for full descriptions see Scott (1979: 558)].

Ecology and distribution pattern (DP): Always associated with rocky areas (mostly “rock islands”), typically in populations of a few to several (to many) individuals. – DP: “rare”; populations scattered and sometimes several kilometers apart (see map, Fig. 6A.)

Dispersal: Fruits, produced in large numbers by each individual, were often found aggregated in small sandy depressions of rock areas. Throwing some of them into flowing water proved that they float well. They asymmetrical shape (see above) enables them to swim like a boat (with the persistent calyx stalk pointing upwards, simulating a boat’s elongated bow). Dispersal by flowing water is, therefore, confirmed here for the first time.

Comments: One of the most conspicuous rheophytes in the study area!

COMBRETACEAE

Combretum trifoliatum Vent. (Fig. 5A–B, 10A–B)

Shrubs often forming large clumps; shoots sometimes showing tendencies to being vine-like. Leaves opposite on plagiotropic shoots but in whorls of 3 on orthotropic shoots. Flowers 5-merous, subsessile, mostly in spike-like, compound terminal or axillary inflorescences. Sepals with a basal tube and broadly-cup-like lobes above, the latter shorter than the tube. Petals white, only slightly longer than the calyx lobes. Stamens 10. Ovary inferior, uniloculate. Fruits (sub)sessile, indehiscent, longitudinally 5-ribbed, conspicuously lobed in transverse section.

Ecology and distribution pattern (DP): Predominantly associated with sandy areas, especially sandy river banks, where plants tend to form huge clumps, from the distance resembling giant cushions; also in rocky areas where a thick layer of sand has accumulated in depressions; populations usually quite large. – DP: “scattered”, primarily because of the scattered distribution of sandy areas.

Dispersal: By flowing water. Tests with the indehiscent, hard but light fruits showed that they float.

Comments: Plants retain their evergreen leaves while submerged (Campbell et al. 2006).

DILLENIACEAE

Tetracera loureiri (Fin & Gagnep.) Pierre ex Craib

For full description see Hoogland (1972: 107–108).

Ecology and distribution pattern (DP): In rocky areas, growing in cracks of rocks; forming smallish populations of up to 10 individuals; associated with “typical” rheophytes such as *Morindopsis* and *Phyllanthus* spp. (see below). – DP: “rare”; only seen in three geographically widely separated areas.

Dispersal: Arillate seeds are presumably bird-dispersed.

Comments: One of the facultative Mekong rheophytes, normally growing in a variety of non-riverine habitats.

EUPHORBIACEAE

Homonoia riparia Lour. (Fig. 4B, 5A–B, 7A, 8G)

For full description and illustrations of flowers and fruits see van Welzen (2007) and Puff & Chayamarit (2007: 58–59).

Ecology and distribution pattern (DP): Found in a wide variety of habitats (both rocky and sandy); sometimes seen in very “low” locations (where plants are partially submerged even when the

Mekong water level is extremely low). – DP: Undoubtedly the most common rheophyte in the study area; usually forming medium-sized to large populations (see map, fig. 6C).

Dispersal: No detailed and confirmed information available. The assumption of a dual mode of dispersal is not unrealistic: The small and light seeds released from the fruits may, on one hand, be blown about by wind and, on the other hand, may also be capable of floating in water.

Comments: Submerged plant parts are leafless; a rise in water level causes a relatively quick loss of leaves. Fig. 7A, documenting a recent fluctuation in water level (a brief flood followed by a drop in water level), shows this well.

EUPHORBIACEAE

Mallotus thorelii Gagnep. (Fig. 11E)

For full description and illustrations see van Welzen et al. (2007: 434–435).

Ecology and distribution pattern (DP): Only seen in rocky areas, growing in cracks of rocks; associated with "typical" rheophytes such as *Syzygium mekongense* and *Artabotrys spinosus*; in small populations of up to 10 individuals. – DP: "rare"; recorded only in a few places, several kilometers apart.

Dispersal: No detailed information available; seeds possibly capable of floating.

Comments: (1) Certainly a facultative Mekong rheophyte. (2) Foliage turning conspicuously red in the dry season (Fig. 11E!).

EUPHORBIACEAE (s.l.; Phyllanthaceae)

Phyllanthus reticulatus Poir. (Fig. 10C-D)

For full description and illustrations see Chantaranothai (2007: 499-500).

Ecology and distribution pattern (DP): Exclusively on moderately steep river banks and in sandbanks, typically associated with *Combretum trifoliatum* and *Homonoia riparia*; in rather small populations of up to ca. 10 individuals. – DP: "rare", only seen in a few well separated locations.

Dispersal: Berries distributed by birds.

Comments: A facultative Mekong rheophyte.

EUPHORBIACEAE

Sauropus heteroblastus Airy Shaw (Fig. 10E–F)

For full description see van Welzen (2007: 537).

Ecology and distribution pattern (DP): Mostly in sand banks but occasionally also in depressed rocky areas where sand has accumulated; normally associated with "typical" rheophytes such as *Homonoia riparia*, *Morindopsis capillaris*, *Hygrophila incana* and *Syzygium mekongense*; usually in moderately large populations. – DP: "scattered"; numerous, well separated populations were observed.

Dispersal: No detailed information available.

EUPHORBIACEAE

Sauropus sp. (cf.) (Fig. 11F)

Small shrub with (sub)erect stems and shortly petiolate narrowly obovate leaves. Foliage resembling *Sauropus heteroblastus* (see above and Fig. 10E-F), but growth form and habitat different. On several occasions invariably seen in sterile state, without any trace of buds, flowers, fruits or old inflorescences.

Ecology and distribution pattern (DP): Always in rocky areas, associated with "typical" rheophytes such as *Syzygium mekongense*, *Morindopsis capillaris*, *Artabotrys spinosus*, etc.; in smallish populations of less than 10 individuals. – DP: "rare", only seen in a few populations several kilometers apart.

Dispersal: No detailed information available.

Comments: This unfortunately incompletely known rheophyte is particularly noteworthy because it appears to be the only one restricted to very low-lying habitats, which are often partially submerged even when the river's water level is lowest in the dry season.

GUTTIFERAE (Clusiaceae)

Garcinia cowa Roxb. ex DC. (Fig. 12A–B)

Functionally dioecious small tree to c. 2–(3) m with yellowish latex. Leaves opposite, petiolate, entire, leathery. Flowers yellowish-orange, terminal and/or axillary, solitary, 4-merous; sepals and petals free, decussate; stamens numerous, in 4 fascicles, connate to petals (present as small sterile stamen fascicles in female morph). Ovary superior, crowned by lobed stigmas (ovary much reduced and sterile in male morphs). Fruit a berry with +/- leathery exocarp; seeds large, embedded in a fleshy pulp.

Ecology and distribution pattern (DP): Only seen in rocky areas, growing in cracks of rocks; associated with "typical" rheophytes such as *Morindopsis capillaris*, Artabotrys spinosus, and/ or *Syzygium mekongense*; in small populations of only a few individuals. – DP: "rare"; recorded only in two places, several kilometers apart.

Dispersal: No detailed information available; possibly fruits are capable of floating.

Comments: A facultative Mekong rheophyte, more commonly growing in a variety of non-riverine habitats.

LABIATAE (Lamiaceae; Verbenaceae in the old sense)

Gmelina asiatica L.

Small shrub or bush with short opposite thorns. Leaves opposite, small, ovate, elliptic or subrhomboid (very variable), glabrous when mature. Inflorescences few- to several-flowered raceme-like panicles, axillary and terminal, nodding or pendulous; bracts usually rather small, linear or lanceolate. Flowers 4-merous. Calyx lobes small. Corolla large, (sulphur-)yellow, 2-lipped; tube curved below, apically widened into a broad ventricose throat, the limb 4-lobed (the lowest largest). Stamens 4; 2 fertile, 2 staminodes. Ovary with 2-lobes stigma. Fruit drupaceous, ovoid to obovoid-pyriform, yellow when ripe.

Ecology and distribution pattern (DP): Exclusively in rocky areas; mostly found associated with *Acacia harmandiana* and *Barringtonia acutangula* populations; populations small, only in groups of 2–5 individuals. – DP: "rare"; only two populations seen, separated by several kilometers.

Dispersal: The drupes are presumably dispersed by birds; also capable of floating in water for some time?

Comments: Certainly not a "typical" Mekong rheophyte.

LECYTHIDACEAE

Barringtonia acutangula (L.) Gaertn. (Fig. 8F)

Shrubs or gnarled trees. Leaves petiolate, simple, with numerous small marginal teeth. Inflorescences terminal, racemose, pendulous, many -flowered. Flowers shortly pedicellate, 4-merous. Calyx small, persistent. Petals red, basally adhering to staminal tube; stamens many in several whorls, filaments long, red (petals plus attached stamens falling off after anthesis). Ovary superior, with red styles and stigmas exceeding the stamens. Fruit 4-angled or shallowly winged (at least when young), with fleshy-fibrous exocarp and woody-fibrous endocarp, 1 seeded.

Ecology and distribution pattern (DP): Exclusively in rocky areas; mostly found associated with *Acacia harmandiana* populations; never seen to form large populations. – DP: "rare"; populations several kilometers apart.

Dispersal: Fruits dispersed by floating.

Comments: Plants retain their evergreen leaves while submerged (Campbell et al. 2006).

LEGUMINOSAE-MIMOSOIDEAE

Acacia harmandiana (Pierre) Gagnep. (syn. *Pithecolobium mekongense* Pierre) (Fig. 13)

Small to medium-sized (to c. 10 m tall) trees with bent stems and "streamlined" crowns facing downstream. For remaining description see Nielsen (1985: 158–160).

Ecology and distribution pattern (DP): Invariably in rocky areas, mostly "rock islands"; typically forming moderately sized populations (ca. 10–30 individuals). – DP: "rare"; populations normally several kilometers apart (see map, Fig. 6A).

Dispersal: In Laos seeds reported as being regularly eaten (and dispersed) by fish (see Table 1 for details and reference).

Comments: (1) With its trunks and crowns bent by the force of the fast flowing river one of the most spectacular rheophytes in the study area! (2) Crowns often are littered with plastic bags, bits of string and broken fishermen's nets (cf. Fig. 12B) – proof that the entire trees are submerged during periods of high water!

LEGUMINOSAE-MIMOSOIDEAE

Mimosa pigra L.

See Nielsen (1985: 151–152) for description.

Ecology and distribution pattern (DP): Mostly seen in sandy habits, often associated with *Homonoia riparia*; never seen to form large populations. – DP: Unlike elsewhere in Thailand, showing no tendencies of becoming a noxious, invasive weed; populations seen were few and far apart.

Dispersal: By fish. In Laos seeds have been found in fish stomachs, and local fishermen report that they are regularly eaten by fish (see Table 1 for details and reference).

Comments: (1) As soon as the water level rises, submerged parts lose their leaves (as in *Homonoia* – see there for details). (2) Presumably the rough environmental conditions in/along the Mekong prevent this American weed from spreading widely.

MORACEAE

Ficus heterophylla L.f. (Fig. 14)

Procumbent shrubs with slender branches, under certain conditions with long bundles of adventitious roots at nodes. Leaves distichous, blades variably shaped, ovate-lanceolate to -elliptic or variously pinnately lobed (juvenile?), margins toothed (to entire); stipules short and inconspicuous, falling soon. Figs pedunculate, axillary on leafy or older leafless branches, solitary, yellowish-orange and smooth when mature, globose to pear-shaped.

Ecology and distribution pattern (DP): Forming large to very extensive populations on flat, sandy areas (often associated with *Homonoia riparia*) or on rather steep, loamy river banks (there being the dominant and often the only taxon). – DP: "scattered"; populations usually many kilometers apart.

Dispersal: In Laos dispersal units have been found in fish stomachs (see Table 1 for details and reference).

Comments: In areas where the plants are obviously submerged for long periods of time (such as low-lying sand-banks (Fig. 14B), the stems always produce long, dangling bundles of adventitious roots (presumably uptaking nutrients directly from the water) at the nodes (Fig. 14D).

MORACEAE

Maclura cochinchinensis (Loureiro) Corner (Fig. 15A–B)

Dioecious scandent low shrubs with glabrous branches (lenticillate when young) bearing straight axillary thorns. Leaves shortly petiolate, blades elliptic to oblong, leathery, glabrous, margin entire, apex rounded to shortly acuminate. Male and female inflorescences axillary, shortly pedunculate, globose. Female inflorescences (formed by laterally fused flowers and bracts) develop into a syncarp, reddish-orange and fleshy when mature, made up of numerous drupelets.

Ecology and distribution pattern (DP): Growing in cracks of rocks, seen associated with *Acacia harmandiana*, *Gymnosporia mekongensis*, *Morinda pandurifolia* and *Streblus taxoides* (see below); populations always small, consisting of a few scattered individuals. – DP: "rare" to "scattered"; populations very far apart.

Dispersal: Syncarps/drupelets presumably dispersed by birds.

Comments: One of the facultative Mekong rheophytes, normally growing in a variety of non-riverine habitats.

MORACEAE

Streblus taxoides (Heyne ex Roth) Kurz (Fig. 15C–D)

Small dioecious thorny shrubs. Leaves shortly petiolate, sometimes variegated, blades elliptic to oblong-lanceolate, leathery, margin entire and apical half crenate or apically with 3 pairs of teeth, apex acuminate to blunt. Male inflorescences axillary, sessile, capitate to shortly racemose. Female inflorescences consisting of 1 pedicellate flower with 4 calyx lobes enlarged and leafy in fruit; ovary straight at first, then oblique, style with 2 stigma lobes. Fruit a small globose drupe, at first enclosed by enlarged foliaceous calyx lobes.

Ecology and distribution pattern (DP): as for

Maclura cochinchinensis (above). – DP: "rare", only 3 small polpuations seen in the study area.

Dispersal: Drupes presumably dispersed by birds.

Comments: One of the facultative Mekong rheophytes, normally growing in a variety of non-riverine habitats.

MYRTACEAE

Syzygium mekongense (Gagnep.) Merr. & L.M.Perry (syn. *Eugenia mekongensis* Gagnep.) (Fig. 4A, 16A-background, 16C–E)

Trees with hardly developed trunks and typically flat much-branched crown appressed to and sprawling over rocks; rarely crown bushy and rounded. Leaves in nature with a blueish-green tinge. For remaining description see Parnell & Chantaranothai (2002: 876-877).

Ecology and distribution pattern (DP): Found in a variety of rocky habitats, including flat rock sheets covered by a thick layer of sediments (Fig. 16D); normally associated with various other typical "rock rheophytes", including *S. thorelii* (see below); usually forming large to very large populations. – DP: "scattered" to "common", i.e. populations typically not far apart.

Dispersal: Fruits are eaten and dispersed by fish. In Laos seeds have been found in fish stomachs (see Table 1 for details and reference).

Comments: (1) One of the most conspicuous Mekong rheophytes in rocky habitats. (2) If this species and *S. thorelii* grow in the same area, the distinction of the two is easy, even from some distance (blueish-green tinged leaves vs. fresh green leaves in *S. thorelii*; see Fig. 16A!). (3) When becoming submerged, the plant's leaves soon become yellowish, die and fall off. Plants in Fig.7B had recently been exposed to a temporary flood (arrow: high water level mark); after the water level had fallen again, the moribund yellowish leaves are exposed again; they will son drop; provided the water level stays low, now leaves will soon develop, independent of season (Fig.7C–D).

MYRTACEAE

Syzygium thorelii (Gagnep.) Merr. & L.M.Perry (syn. *Eugenia thorelii* Gagnep.) (Fig. 4B, 16A-foreground, 16B)

Trees with hardly developed trunks and typically flat much-branched crown appressed to and sprawling over rocks. Leaves in nature fresh green. For remaining description see Parnell & Chantaranothai (2002: 905).

Ecology and distribution pattern (DP): Confined to rocky habits; usually forming relatively small populations. – DP: "scattered"; populations often several kilometers apart.

Dispersal: Most probably dispersed by fish as in *S. mekongensis* (see above).

Comments: (1) Much less common than *S. mekongensis*.

RUBIACEAE

Morindopsis capillaris (Kurz) Kurz (Fig. 4E)

For full description and illustrations of flowers and fruits see Puff & Chayamarit (2008).

Ecology and distribution pattern (DP): Usually associated with various rocky areas (flat rock sheets, between boulders, etc.); growing in cracks of rocks. – DP: "rare"; populations small (often solitary plants only, or only few, scattered plants in a given rocky habitat), normally several kilometers apart (see map, Fig. 6B)

Dispersal: see Puff & Chayamarit (2008: 79). In Laos dispersal unites reported as being regularly eaten (and dispersed) by fish (see Table 1 for details and reference).

Comments: One of the most easily over-looked rheophytes as it does not occur in large, dense populations; solitary individuals frequently grow in between plants of large population forming rheophytes such as Homonoia riparia or *Syzygium* spp.

RUBIACEAE

Morinda pandurifolia Kuntze (syn. *Morinda longifolia* Craib) (Fig. 15E–H)

Small shrubs with opposite, often hetero-phyllous leaves: at least some of the blades pandu-rate (fiddle-shaped to +/- lyrate; Fig. 15G), the remaining elliptic to lanceolate (in the study areas less commonly all leaf blades elliptic to lanceolate). Inflorescences consisting of terminal, solitary capitula composed of several to +/- many flowers fused by their ovaries. Flowers white (pinkish tinged in bud), 4–5(–6) merous, hermaphrodite, heterostylous. Corolla with an often slightly curved tube, lobes recurved. Stamens included and with short filaments (long-styled morphs) or exserted and with long filaments (short-styled morphs). Style with 2-lobed stigma exserted (long-styled morph) or included (short-styled morph). Capitulum in fruiting stage forming an infructescence or "syncarp" consisting of numerous 1-seeded pyrenes.

Ecology and distribution pattern (DP): In rocky areas, deeply rooted in cracks of rocks; not uncommonly in depressed rocky areas where a thick layer of sediments accumulates (see Fig. 15F). – DP: "scattered"; typically in populations of few to several (many) individuals, often several kilometers apart.

Dispersal: Infructescence or "syncarp" presumably initially water-dispersed. Hydrochory is confirmed for *Morinda citrifolia* (in its natural habitat a coastal plant!); in this species floating properties are improved by the presence of air-filled chambers in the pyrenes' endocarps (Ulbrich 1928: 143). In Laos dispersal unites reported as being regularly eaten by fish (see Table 1 for details and reference).

SALICACEAE

Salix tetrasperma Roxb. (Fig. 8G)

For full description see Larsen (1987: 122).

Ecology and distribution pattern (DP): Usually in sandy areas such as moderately steep river banks and in accumulated sand in depressions of rocky regions. – DP: "scattered"; populations usually small, sometimes only consisting of 4–5 individuals, often several kilometers apart.

Dispersal: Seeds, with their tufts of hairs, are anemochorous.

Comments: Easily overlooked when growing in between large *Homonoia* populations (unless when wind exposes Salix' silvery leaf surfaces – see Fig. 8G).

RHEOPHYTES conspicuously MISSING in the study area

After the study of the above list, anyone moderately familiar with rheophytes in Thai rivers and streams will have noted that certain rheophytic taxa which are frequently and commonly seen elsewhere, are not recorded from the stretch of Mekong studied. "Absentees" include primarily herbs (i.e., mostly "torrenticolous rheophytes") such as *Cryptocoryne* spp. (e.g. *C. crispatula**, Araceae), or various Podostemaceae*, but also some (low) shrubs such as some *Ficus* spp. (e.g. *F. pyriformis*, Moraceae), *Calophyllum pisiferum** (Guttiferae), *Kailarsenia lineata* (Rubiaceae), or the low rheophytic *Pandanus humilis** (Pandanaceae) [taxa marked with * illustrated in Puff & Chayamarit (2006)]. Rheophytic ferns appear to be completely absent. As it seems highly unlikely that all of those would have been overlooked during field work, the most reasonable explanation (or guess) for their absence might be the exceptionally rough environmental conditions in which Mekong rheophytes must survive. It can be imagined that especially the herbaceous rheophytes will have difficulty in persisting in a submerged state for several months (as opposed to much shorter periods elsewhere); the, in part, very fast flowing river, may be disadvantageous as well.

DISCUSSION

Comparisons with Mekong rheophytes outside the study area

It is clear that the survey of study area is not (and cannot be) fully complete. The complexity of the rocky areas and the difficult terrain, in combination with the fact that, because of the habitual similarity of many rheophytic taxa, the vegetation must be studied from close distance, would have necessitated many more visits during the low water period, and visits of every single potential habitat, no matter how small. This would have taken many years. In spite of this obvious shortcoming we nevertheless believe that the present study is representative. The important question that arises is: How does the here reported rheophyte composition of the studied section of the Mekong compare to that found elsewhere? ["elsewhere", on the one hand, means the entire lower Mekong (particularly southern Laos and northern Cambodia) and, on the other hand, the river North of the study area where it forms the common border between Thailand and Laos (almost another 600 km!)].

Figure 7. Phenology of selected taxa: *Homonoia riparia* (A) and *Syzygium mekongense* (B–D) as examples for deciduous rheophytes. A–B. An earlier short-time flood followed by a drop in water level reveals that leaves turn brown and drop when becoming submerged (note the difference to the plants growing higher up in B; the arrow indicates the flood water level). C. Plants starting to produced new leaves after the water has receded. D. View of "crown" with fresh, not fully developed leaves. (In A, clumps of *Combretum trifoliatum* visible on the sandy river bank; above them plantations). All photographs C. Puff, taken in June.

Figure 8. A–D. *Artabotrys spinosus*; A, in “rock island” and B, on sandy-rocky shore; C, flower; D, young fruit (note spine; arrow). E. *Crateva magna*, juvenile (*Syzygium mekongense* in background). F. *Barringtonia acutangula*. G. *Homonoia riparia* and two individuals of *Salix tetrasperma*, recognizable by the silvery lower surfaces exposed by strong wind. All photographs C. Puff.

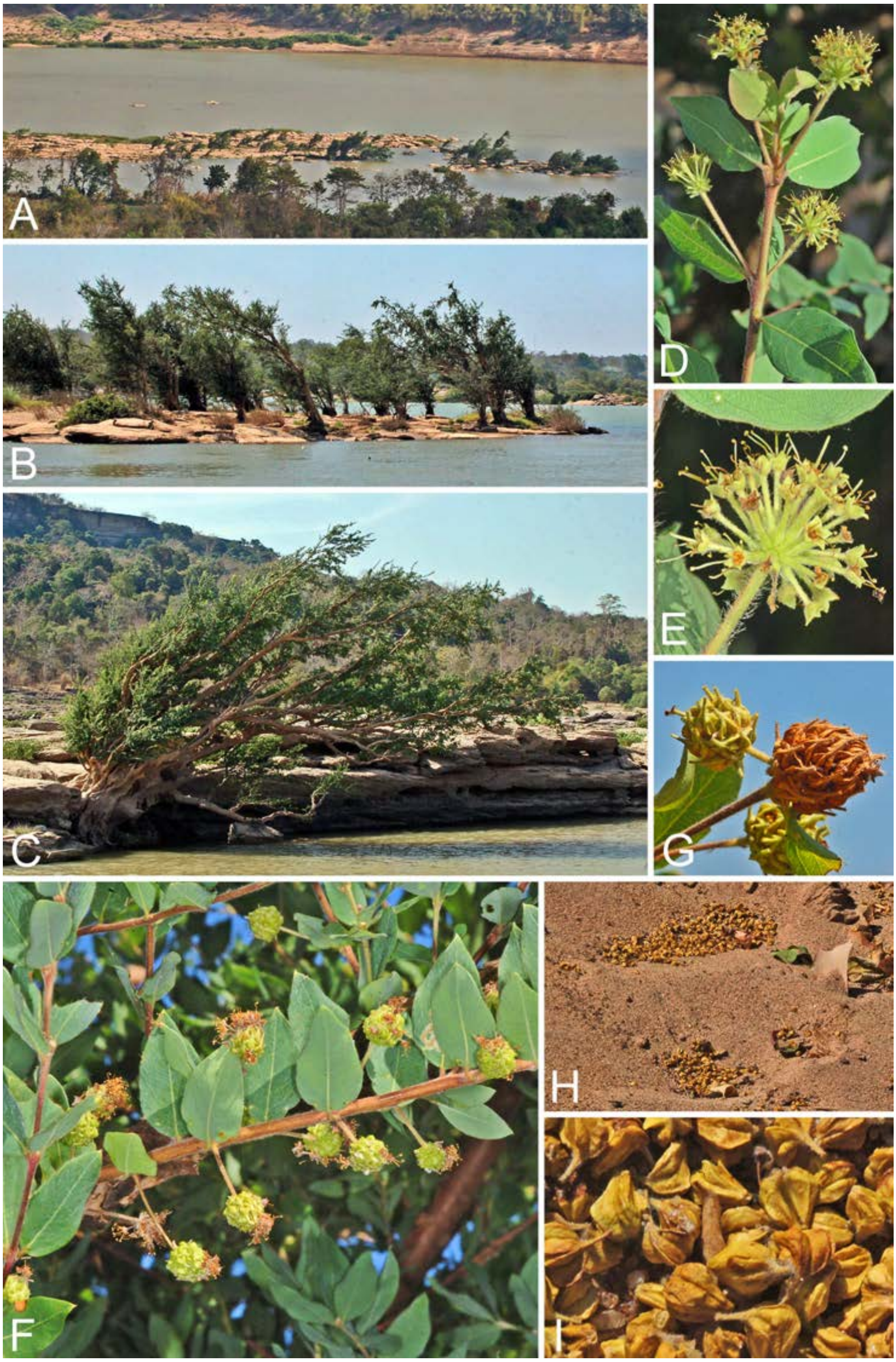

Figure 9. *Anogeissus rivularis*. A–B, two populations (A, as seen from Pha Mon viewpoint, Pha Taem National Park ; B, from "rocky island" near Moon R. – Mekong confluence, (see Fig. 3C); C. individual tree from population A; D–E. inflorescences, just after flowering; F, immature fruiting heads; G. mature fruiting heads, each consisting of tightly adpressed individual fruitlets; H, dispersal units in the riversand, I, detail (see text for details). All photographs C. Puff.

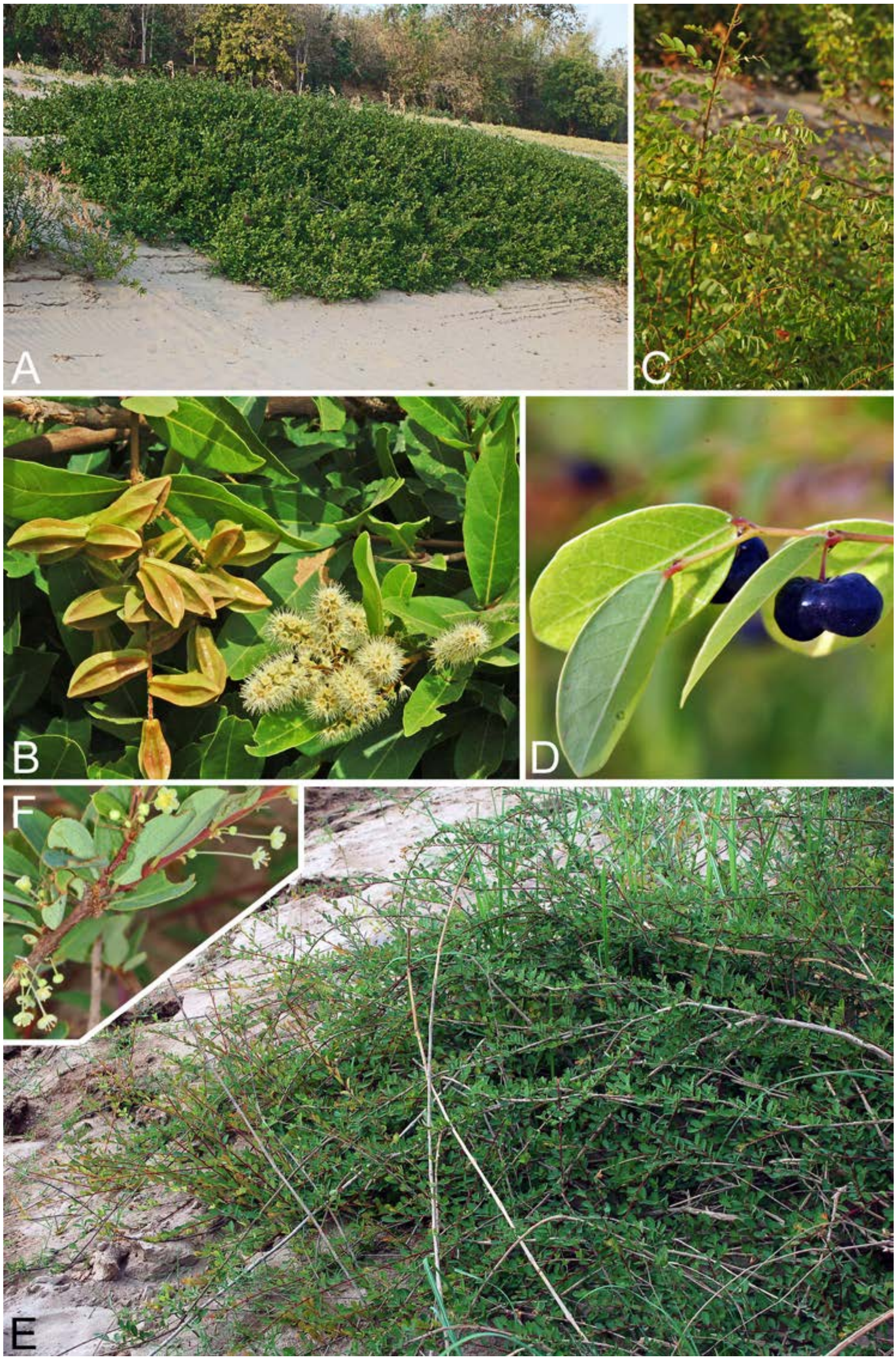

Figure 10. A–B. *Combretum trifoliatum*; A, on moderately steep sandy river shore (see Figure 5A–B); B, flowers and fruits. C–D. *Phyllanthus reticulatus*; C, from same habitat as A; D, fruits. E–F. *Sauropus heteroblastus*; E, habit (sandy-rocky); F, inflorescences and flowers. All photographs C. Puff.

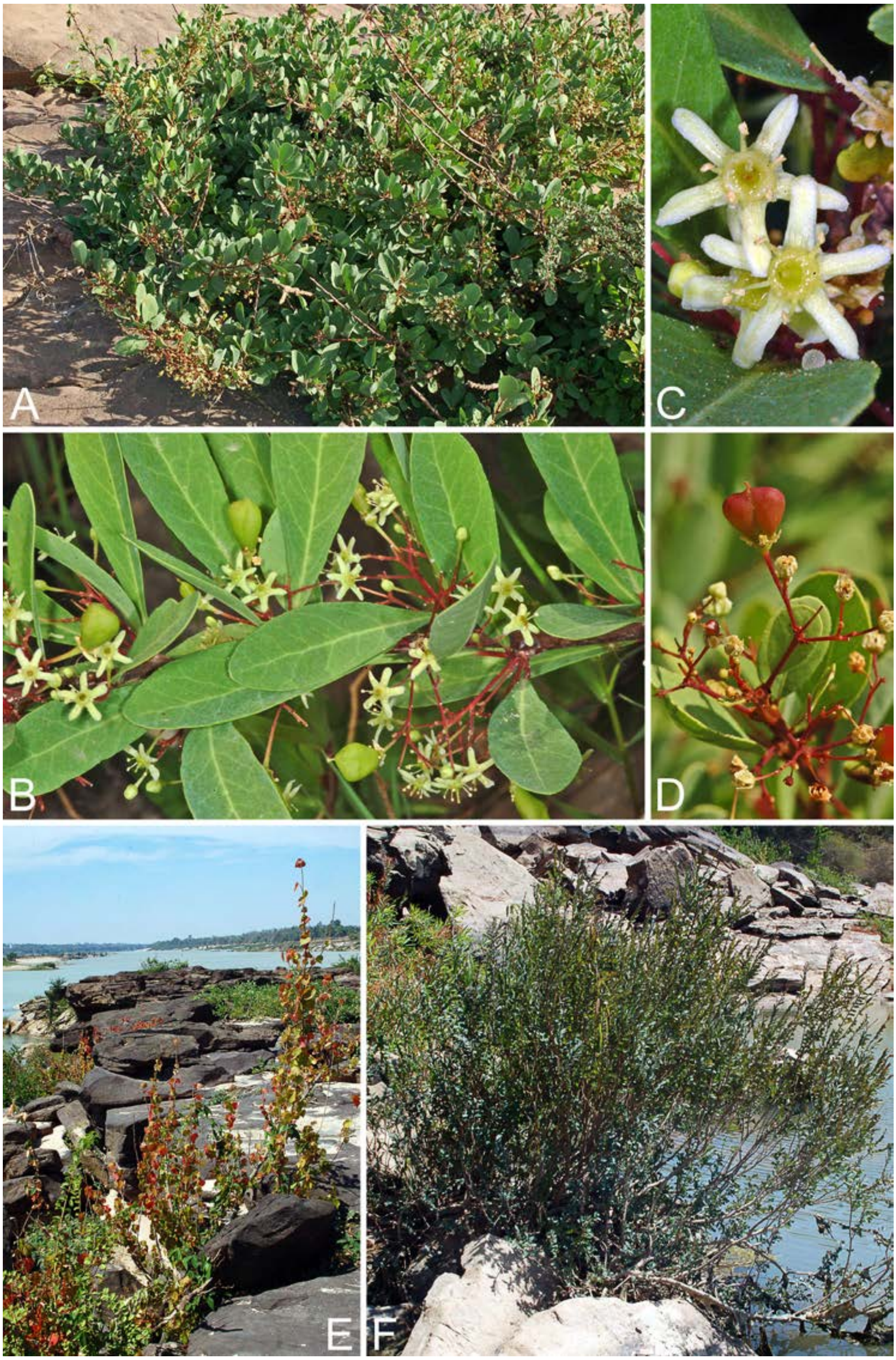

Figure 11. A–D. *Gymnosporia mekongensis*; A, habit; B, twig with inflorescences; C, male flowers; D, inflorescence with (immature) fruit. E. *Mallotus thorelii*, habit, plants always with red old foliage. F. *Sauropus* sp. (cf.) (Euphorbiaceae), habit. All photographs C. Puff.

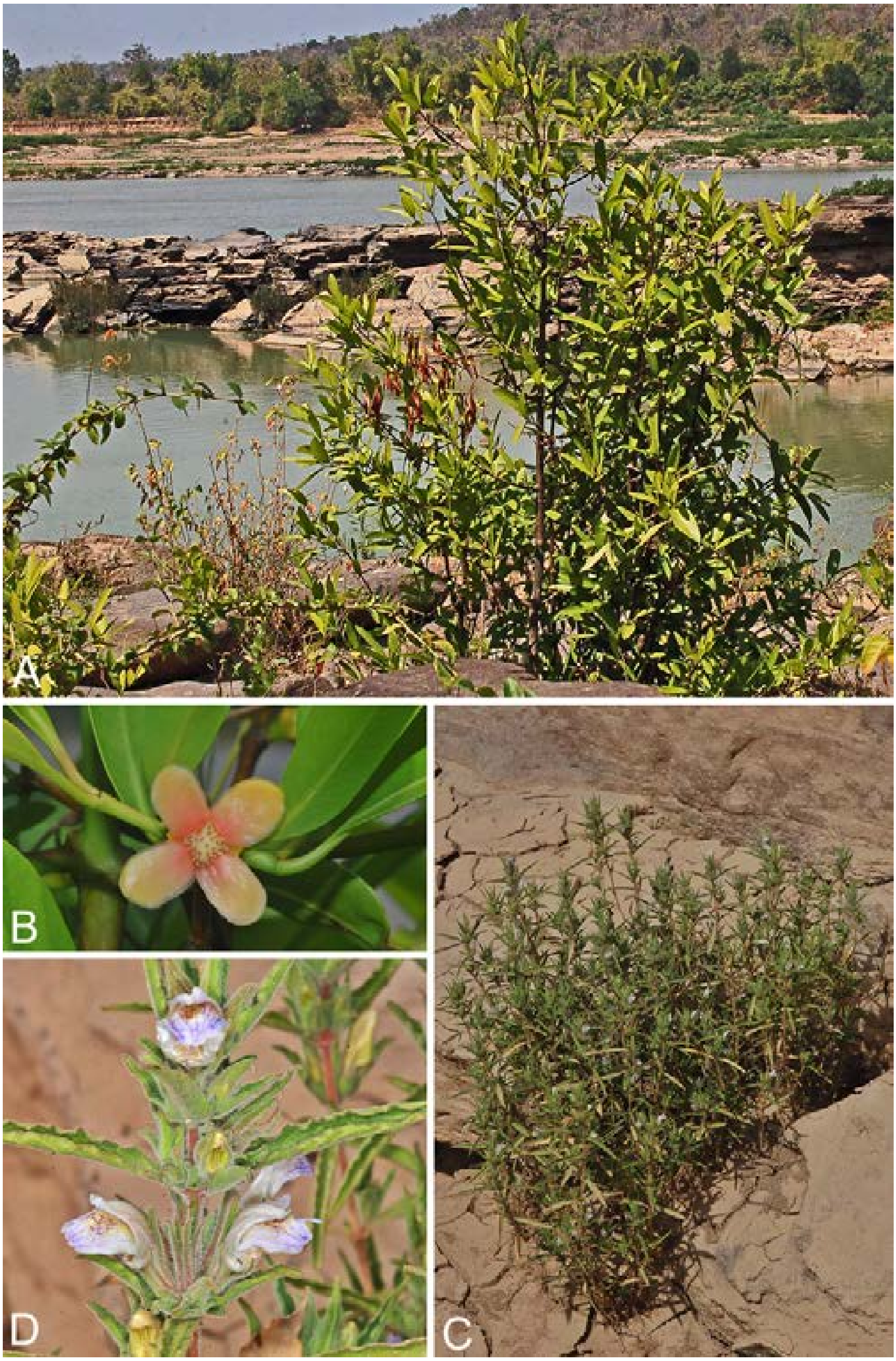

Figure 12. A–B. *Garcinia cowa* (Guttiferae); A, habit and habitat; B, male flower. C–D. *Hygrophila incana* (Acanthaceae); A, habit; B, flowers. All photographs C. Puff.

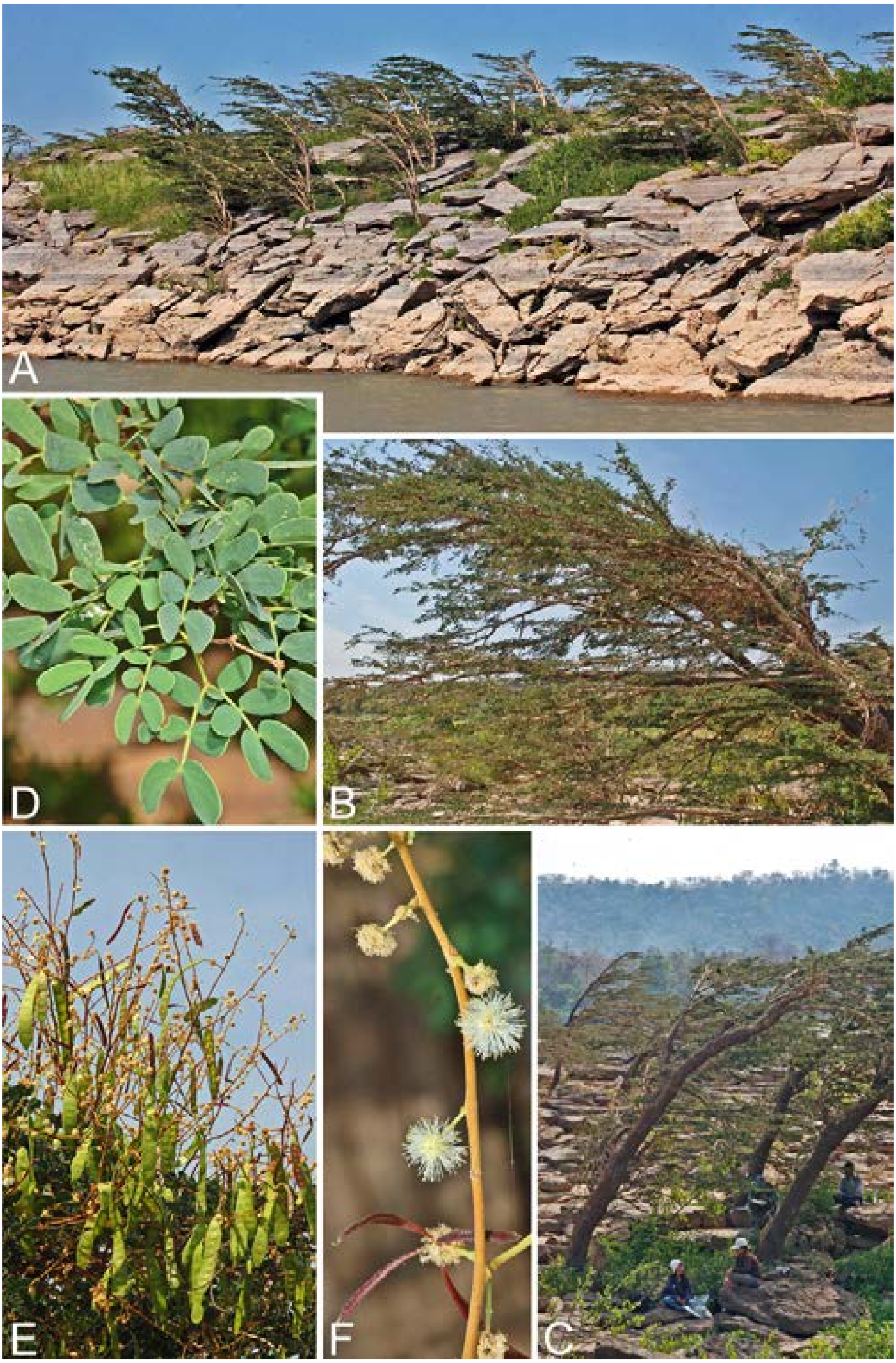

Figure 13. *Acacia harmandiana*. A–C. plants growing on "rock islands" (A and B–C, respectively, from different populations; crowns pointing downstream); D. foliage; E. inflorescences and almost mature pods. F. portion of inflorescence with flowering heads and very young fruits. All photographs C. Puff.

Figure 14. *Ficus heterophylla*. A. population on loamy river bank; B–D. population on small sandbank; B, some *Homonoia riparia* plants in background; C, foliage, note heterophylly; D, stem with long, bundled adventitious roots exposed in the dry season. All photographs C. Puff.

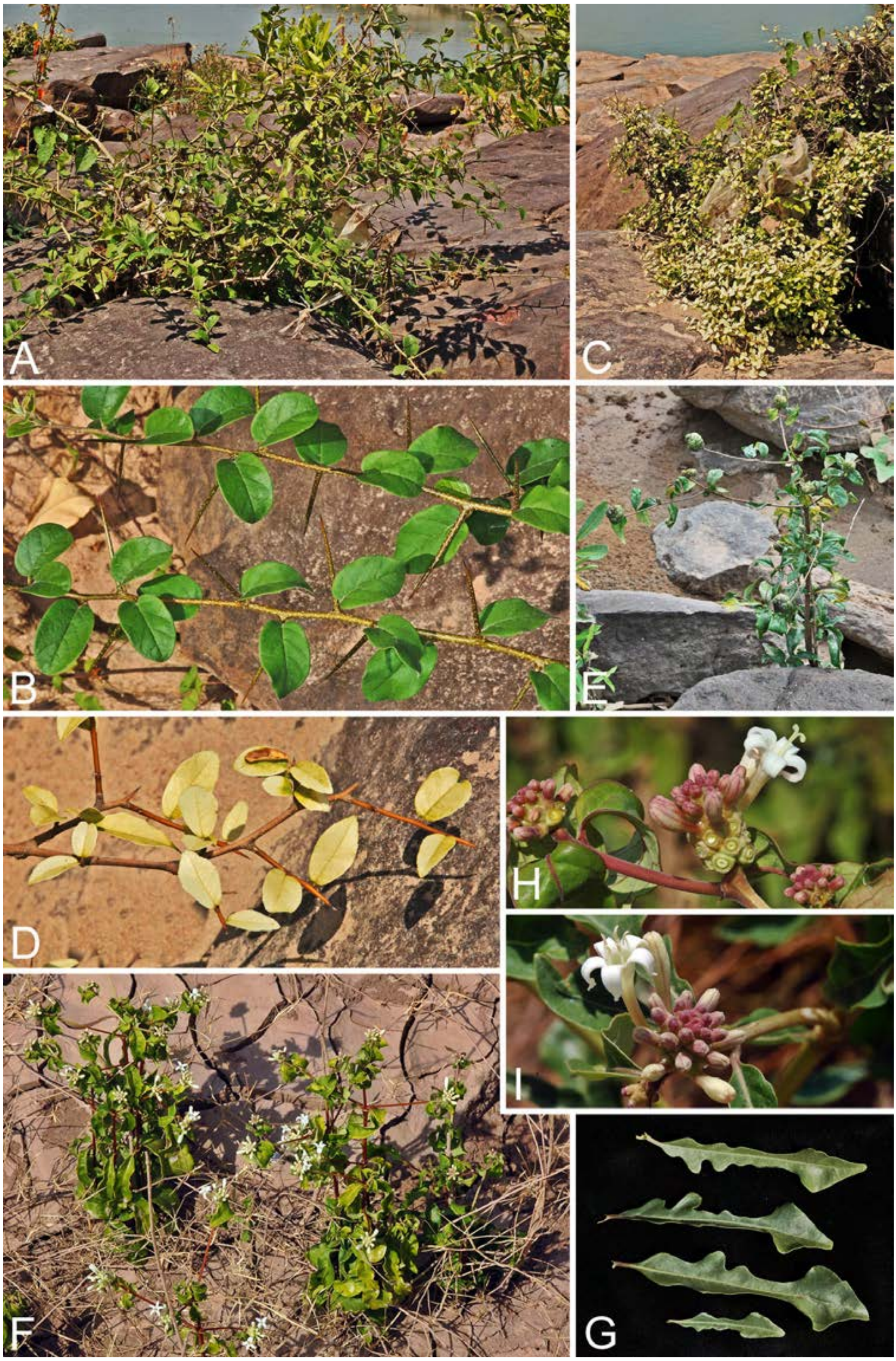

Figure 15. A–B. *Maclura cochinchinensis*; A, habit; B, lenticellate branches with short shoot thorns. C–D. *Streblus taxoides*; A, habit; B, branches with leafy short shoot thorns. E–I. *Morinda pandurifolia*; E, fruiting plant in rock cracks; F, flowering plants growing rocky area thickly covered by dried, cracked mud; F, pandurate leaves; H, long-styled and I, short-styled flower. All photographs C. Puff.

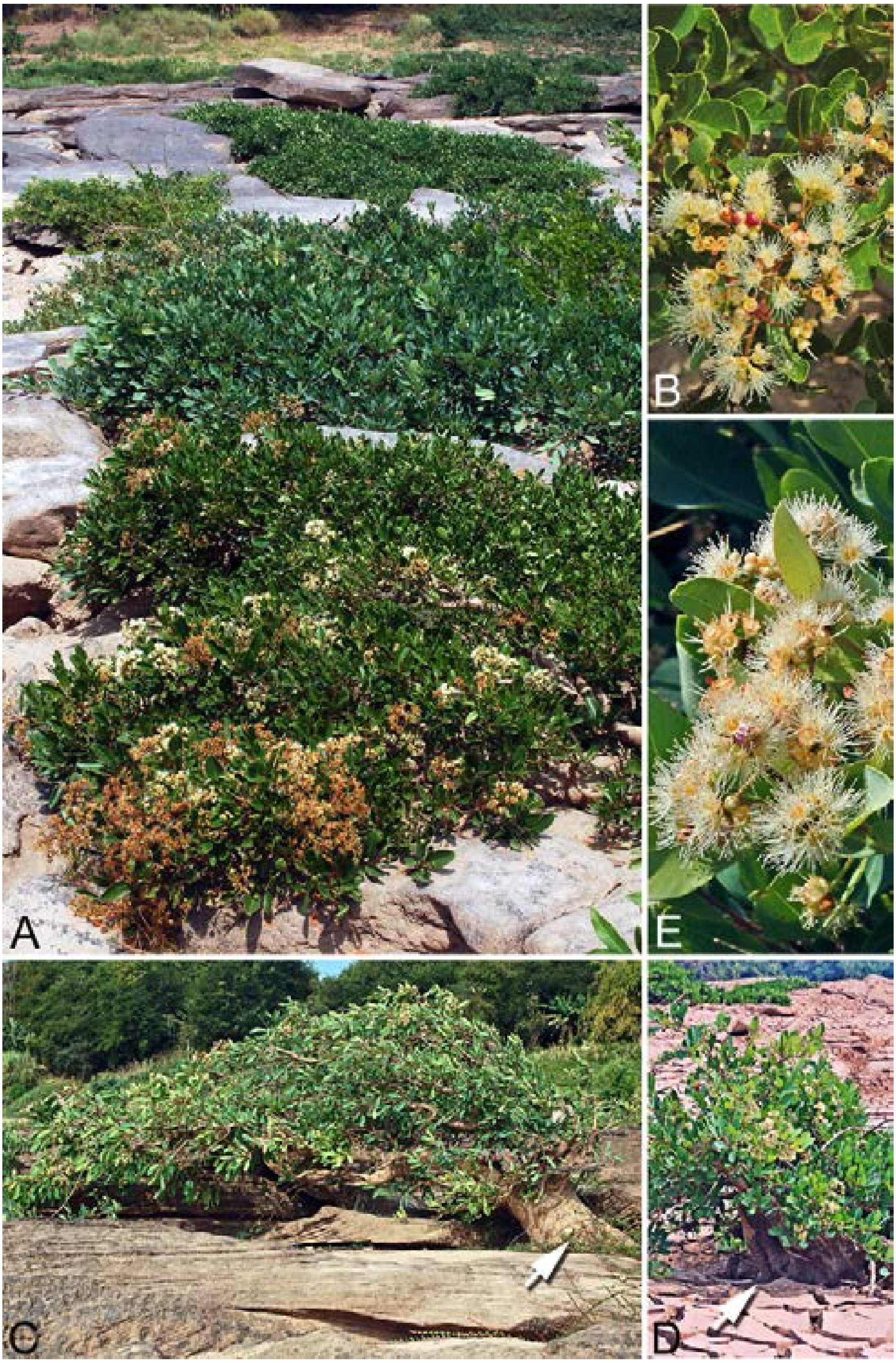

Figure 16. *Syzygium species*. A. *S. thorelii* in the foreground and *S. mekongense* in the background (distinguishable by foliage with a slight bluish tinge). B. *S. thorelii*, flowers. C–E. *S. mekongense*, C–D, habit, note almost non-existent trunks (arrows), crown spread over rocks (C), and small bushy crown (D; plant growing between rocks thickly covered by dried, cracked mud); E, flowers. All photographs C. Puff.

Comparisons, at this stage, are difficult, simply because here are no detailed studies. There is one exception, however: Thanks to attempts to develop the so-called "Siphandone Wetlands" as a major tourist attraction, internationally funded thorough and diverse studies have been carried out. The region (meaning "4000 islands") lies about 200 km South of the study area, in Laos' southern Champasak Province (see map, fig. 2 in Baird 2007). Here, the main Mekong river splits up into a complex system of channels (with islands in between); there are also rapids and a series of waterfalls (Khone Falls), and areas with deep water pools. The southernmost part of this region also extends into northeastern Cambodia, notably Stung Treng Province, but comparable areas occur as far South as Kratie Province (Altobelli & Daconto 2001). In a simplified classification of the vegetation of the Siphandone Wetlands, Baird (2007) distinguished two categories of "flooded forest" both of which are characterized by plants (mostly trees and shrubs) which are "adapted to survive up to six months of total or partial inundation during the rainy season between May and October when water levels rise from 6 to 8 meters" (Altobelli & Daconto 2001). The situation thus is fully comparable to that in the area of the Mekong studied by us (for a full survey of the vegetation, including rheophyte areas, see Maxwell 2001a). While it was to be expected that a certain number of rheophytes in the Siphandone Wetlands and in the PTNP study area are the same, an analysis of the flora (Maxwell 2001b) revealed a surprisingly high percentage (60 %) of common occurrences. If herbaceous taxa (which are conspicuously absent from PTNP) are excluded, the percentage is even higher 68% (see Table 2).

With regard to the distribution of rheophytes upstream from the PTNP study area there is only very fragmentary information. Apart from "common" rheophytes (e.g. *Homonoia riparia*!), there are also examples of taxa whose distribution has been classified as "scattered" and "rare" in the present study, which extend further North: The type of *Morindopsis laotica* (a synonym of *M. capillaris*), for example, is from "Paklai" (Pak Lay, Vientiane Prov.), and in Thailand the species has also been collected in a locality in Nong Khai Province. *Artabotrys spinosus*, listed as a Thai threatened plant, has also been recorded from Loei (Pakchom) and Nong Khai Provinces (Pooma 2005: 5) and in Mukdahan Prov. (North of Khemmarat; pers. obs. CP). *Anogeissus rivularis*, a characteristic species in Siphandone Wetlands [Chamapasak Prov.; apart from the type, which is from adjacent Attapu Province (not on the Mekong), the only known locality in Laos (Newman et al. 2007)], has several populations in the study area but was also observed by C.P. further North, near Khemmarat (Mukdahan Prov.) [a Kerr collection from "Kemarat, Ubon" at Kew was mentioned by Grey-Wilson (1971: 146) as being "the first record of the genus in Thailand"]. *Syzygium thorelii*, too, is known from Khemmarat (type locality; Parnell & Chantaranothai 2004); the species has, however, been collected even further North (Pak Chom, Loei Prov., *Pooma et al. 4072*, **BKF!**) (recorded in the flora treatment).

There are, of course, also Mekong rheophytic taxa which were not recorded in the study area but are know from more northern localities: a good example in place is *Cephalanthus stellatus* (synonym of *C. angustifolius*, Rubiaceae), so far only known from the type locality ["banks of Mekong at 16° N"].

A plea to collectors: please make precise habitat notes

"In the first place recognition of rheophytes depends upon the attention which the field botanist pays towards the ecology of the plants he collects during trips. Even today this leaves much to be desired… A dedicated, scientific collector … should give a clear indication of the habitat, and extend his field observations of a riverbed plant to whether the species is also found beyond the flood mark…" Van Steenis' (1981, repeated in 1987) words, unfortunately, are still valid today. Most of the available BKF specimens from the Mekong do not give any indication as to where the plant were actually collected; labels indicating that a collected plant is a rheophyte are extremely sparse. Habitat notes such as "stream", "along river", etc. are hardly useful. Also notes on a plant's adapted and modified habit (see, for example, *Acacia harmandiana*, fig. 13A–C, whose strongly bent stems and "streamlined" crowns are obviously due to the power of the flowing river) are almost totally lacking. In the

Table 2. Comparison of rheophytes present in the study area (PTNP) and in the Siphandone Wetlands (SW) (Champasak Prov., Laos); data from the latter compiled from Maxwell (2001b). – Authors and family names only given for taxa not in the "list of observed rheophytic taxa"; simplified growth forms (GF): H – herb, S – shrub (S/H – shrubby herb), T – tree (S/T – shrubby tree , shrub or tree).

Taxon	GF	PTNP	SW	Note
Acacia harmandiana	T	x	x	
Anogeissus rivularis	T	x	x	
Barringtonia acutangula	T	x	x	
Blachia cotoneaster Gagnep. (Euphorbiaceae)	S		x	
Ceratophyllum demersum L. (Ceratophyllaceae)	H		x	
Combretum trifoliatum	S	x	x	
Crateva magna	T	x	x	
Cryptocoryne tonkinensis Gagnep. (Araceae)	H		x	
Ficus heterophylla L.	S	x	x	
Gymnosporia mekongensis (Pierre)	S	x	x*	as "*Maytenus* (*Gymnosporia mekongensis* Pierre)"
Homonoia riparia	S	x	x	
Hygrophila incana	H/S	x	x	
Meniscium proliferum (Retz.) Sw. (Thelypteridaceae)	H		x	
Mimosa pigra	S	x	x	
Morinda pandurifolia	S	x	x	
Phyllanthus jullienii Beille (Euphorbiaceae)	S/H		x	
Phyllanthus reticulatus	S	x	x	
Polyalthia modesta (Pierre) Fin. & Gagnep. (Annonaceae)	S		x	
Polygonum flaccidum Meissn. (Polygonaceae)	H		x	
Rotula aquatica Lour. (Boraginaceae)	S		x	
Salix tetrasperma	S/T	x	x	
Sauropus heteroblastus	S	x	x	
Syzygium mekongense	T	x	x*	as "*Eugenia mekongensis* Gagnep."
Syzygium thorelii	T	x		
Telectadium edule H. Baill. (Asclepiadaceae)	S		x	
Xantonnea parvifolia (O.K.) Craib var. *salicifolia* (Pierre ex Pit.) Craib (Rubiaceae)	S		x	

Myrtaceae treatment for Flora of Thailand (Parnell & Chantaranothai 2002), one will search in vain for *Syzygium* species with reduced stems and flattened, cushion-like crowns spreading over rocks (such of those illustrated in Fig. 7B–D and 16); species are almost invariably described as "Tree to … m," "Shrub or small tree to … m" or "Shrub to … m". Accurate field notes would have enabled the authors to make a more meaningful habit description. The ecology of one of the most fascinating and prominent "key" rheophytes, *Acacia harmandiana*, is given as "bamboo jungles, deciduous and dry deciduous forests, savannas," without any mention of its rheophytic habit (although the species' synonym *Pithecelobium mekongensis* would been a good clue) (Nielsen 1985).

Collectors are therefore once again urged to improve their note taking and provide precise detail. Users of floras, field botanists, foresters and interested laymen will greatly appreciate these efforts.

Dam building – the death of fascinating Mekong rheophytes?

As there persistent rumours that the construction of a huge dam situated within the study area is in the planning stage, the question arises what will be the effects on the unique rheophyte populations? One of the aims of building a dam is to raise the general water level to create a continuous waterway for ship traffic. At the moment, this is not possible in the low water (dry) period because of rapids in various places (which at the same time are major rheophyte habitats!); currently only small boats are able to pass. Raising the water level so that rapids are no longer pose a threat to ship traffic, consequently, means that these habitats will be permanently destroyed. The same holds true for other rheophyte habitats such as "rock islands" (the habitat of the unique *Acacia harmandiana* poulations; Fig. 13A) or huge rock shelves, etc.

The consequences of this habitat destruction cannot be forecast with full certainty. The worst – or most negative – scenario is that many of the rheophytes in the area will disappear completely. If one were more optimistic, it could be assumed that rheophyte will start to inhabit habitats "newly available" after the raise in water level. Several question marks, however, remain: (i) will there be sufficient suitable "substitute habitats" such rocky places, once the original ones are no longer available (it appears doubtful). (ii) Will rheophytes be able to establish themselves "fast enough" in substitute habitats once their original one have disappeared. It is totally unknown whether this could happen, as detailed studies concerning the establishment of rheophytes (and the time needed for successful establishment) are lacking altogether.

The interested reader is referred Lytle & Poff (2004) who address the problem of flow regime alteration caused by, for example, large dam projects in great detail.

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