

Rheophytes in South Africa

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ABSTRACT

The bio-ecological class of rheophytes, species restricted to swift-running streams below flood level, is for the first time recorded for South Africa. A preliminary list is made of representative species.

RÉSUMÉ

DES RHÉOPHYTES EN AFRIQUE DU SUD

Ceci constitue la première mention pour l'Afrique du Sud de la classe bio-écologique des rhéophytes, espèces limitées aux cours d'eau rapides en-dessous de leur niveau de crue. Les espèces représentatives font l'objet d'une liste préliminaire.

In 1932 I coined the term rheophytes for species which are confined to streambeds within the approximate flood level, where they occur under torrential conditions in rapids, cascades and on gravel and sand bars, and even in fairly slow streams. The term has probably not been used before in Africa, but I have recorded rheophytes in Malesia and subsequently (1952) on a more methodical basis in Australia.

Rheophytes fall into two classes, those of waterfalls and torrents to which belong the Podostemonaceae and Hydrostachyaceae, while the second class consists of normal, perennial, mostly woody plants which are adapted to withstand swift currents when a river is in spate.

It is about the latter class that I wish to make some observations. First of all, I should mention that these plants are found in most classes of the Cormophytes, including ferns, monocots and dicots (Fig. 1), as is the usual pattern with biological assemblages of life-forms, e.g. myrmecophytes, parasites, saprophytes, etc. In several cases, all species of a genus belong to the rheophytes, but these genera are mostly monotypic or small; in most cases, however, it is just one or a few species of one genus which are restricted to a rheophytic habitat and have the characters of a rheophyte.

These characters I have defined (1952) as follows:

(i) Strong and wide root-system able to anchor in moving gravel and boulders, or very thick root-matting to adhere to rocks.

(ii) Tough, flexible structure of stems and stalks to enable to withstand the draw of a swift current.

(iii) Almost invariably lanceolate or even narrower leaves or leaflets, often resembling in shape those of willows.

(iv) Sometimes peculiarities of seed or fruit, season of fruiting and seeding, germination and dispersal to maintain the habitat.

Rivers are the gutters of nature and also receive, of course, apart from all kinds of debris, the diaspores of many land species. This constant supply does not lead to permanent establishment, because of a lack of the necessary equipment mentioned above, except for the true rheophytes which lead their whole life-cycle in the streambed within flood level parameters.

It appears that rheophytes, which are all perennials, herbaceous or shrubby, are characterized by narrow, willow-like leaves (or leaflets) which are frequently falcate with a leaf index of at least 3, more often a higher figure. Beccari, who first noticed this class in the rapids of Bornean rivers, called them "stenophyllous plants" and so did Ridley who found them in Malayan.

Epithets of rheophytes often refer either to their narrow leaf-shape, their habit, or their habitat. Furthermore, the habit of rheophytes is mostly broom-like, umbrella-shaped, or table-shaped, caused mostly by sympodial, often virgate branching. The crown is often oblique and elongated in the direction of the stream. Furthermore, it appears that in genera which have normally pinnately compound leaves the number of leaflets is often reduced to 3 or even to 1. This occurs, for example, in the Meliaceae genera *Aglaia* and *Dysoxylum* in Malesia.

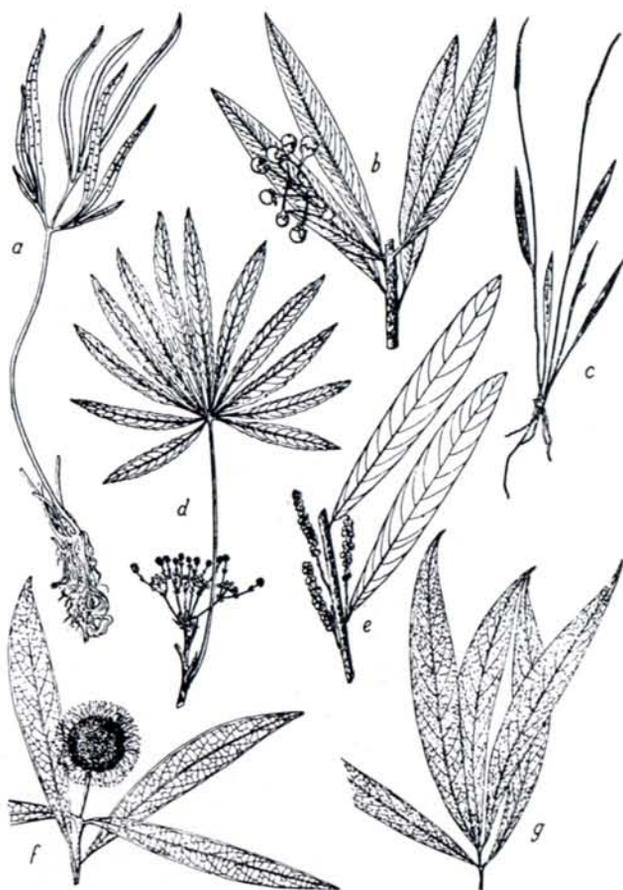


Fig. 1. Malaysian rheophytes: stenophyllous foliage as a common morphological 'adaptation' in systematically remote plants. a. *Nephrodium stenophyllum* BAKER (*Polypod.*), b. *Ardisia tahananica* K. & G. (*Myrs.*), c. *Ophioglossum inconspicuum* v.A.v.R. (*Ophiogl.*), d. *Boerlagiodendron borneense* (SEEM.) MERR. (*Aral.*), e. *Homonoia riparia* LOUR. (*Euph.*), f. *Neonauclea chalmersii* (F.V.M.) MERR. (*Rub.*), g. *Aglaia ijzermannii* BOERL. & KOORD. (*Meliac.*). All $\times \frac{1}{3}$, except d, $\times \frac{1}{4}$.

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Generally, leaves of rheophytes are glabrous with very few exceptions. Furthermore, the leaf margin of rheophytes is usually entire and only rarely slightly crenate.

This tendency towards a simple, willow-like leaf results in a decreased resistance to swift running water: what happens is that in swift-running water the leaves of the twigs together form a streamlined whole—an ovoid-attenuated body, formed by the flexible narrow leaves.

The habit is difficult to describe, but is most characteristic: in random collections one can immediately spot rheophytes if one is acquainted with them and usually there is some debris present between twigs resulting from inundation. In Fig. 1 the leaves of some Malesian species of rheophytes are illustrated.

Rheophytes occur in many families, Euphorbiaceae, Rubiaceae and Myrtaceae being richest.

They are found almost everywhere in the world, the everwet tropics being the most richly endowed with them, especially the small streams with a fairly high gradient. However, several occur under seasonal climatic conditions and even under semi-desert conditions in streambeds or wadis, which are infrequently flooded, as for example the desert willow of southern North America, *Chilopsis linearis* (Cav.) Sweet of the family Bignoniaceae. In all several hundreds are known, among them also some ferns.

They are mostly sorted into gradient classes, quite frequently occurring in one river system, certain species being more adapted to conditions of high gradient in river tracts with large boulders, others preferring gravel or sand.

As to their size, most rheophytes are either perennial herbs or smallish bushes or shrubs, sometimes small trees, while in exceptional cases they grow to tall trees.

Although growing in streambeds most commonly along their margin below flood level, rheophytes are not waterplants (hydrophytes), although a few hydrophytes can be referred to this class. These hydrophytes mostly possess ribbon-like leaves. Apart from these few hydrophytes, and Podostemonaceae and Hydrostachyaceae, rheophytes can easily be grown on dry land and even a few well-known cultivated plants belong to them, apart from the willows, for example *Nerium oleander* L. But in nature they are restricted to the streambeds. Even the two families just mentioned cannot conceal their derivation from land plants, as they develop only in their vegetative stage submerged in water; their flowering and fruiting takes place in the short dry or less wet period when the water level has receded.

Single rheophytes of larger genera must have evolved from land species. This evolutionary process probably took place in a gradual way. The first stage may have been that part of a population segregated in invading streambeds and acquired adaptations to this habitat. The invaded niche, consisting of bare gravel, rocks or coarse sand was empty and there was no vegetation to compete with; it offered only the challenge to withstand being flooded by swift-running water and being swept away. If this was successful, probably a first adaptation was acquired, viz. the adoption of willow-like leaves, toughness of leaves and twigs, and development of a large root-system for anchorage. The mastering of the habitat conditions caused a considerable increase in the population invading the streambed, while leaving only a small part of the population outside it to compete with other riverine or gallery forest vegetation.

In South Africa this situation exists for example in *Combretum caffrum* (Eckl. & Zeyh.) Kuntze (syn. *C. salicifolium*), *Nuxia oppositifolia* (Hochst.) Benth. and *Rhus montana* Diels var. *gerrardii* (Harv. ex Engl.) R. Fernandes.

In some other cases, specialization has gone somewhat further in that there is a distinct riverine population, which can be distinguished as a variety or subspecies. Once this ecological segregation has taken place, it is not far-fetched to assume that such early stages may have led to further speciation in ecological isolation by habitat, and proceeded as far as generic rank. In fact, there are some genera confined to streambeds as rheophytes. In general, such genera are monotypic, but there are rheophyte genera with more than one species which are all confined to streambeds. In Elaeagnaceae there are even two genera, *Shepherdia* and *Hippophaë*, which are almost exclusively rheophytes while in the third genus of the family, *Elaeagnus*, a rheophytic species exists in south-eastern Asia. The families Podostemonaceae and Hydrostachyaceae are entirely rheophytic and must date from very ancient rheophytic ancestry.

There are sometimes difficulties in deciding which are true rheophytes and which are not. This decision can only be made by observations of local botanists with field experience and access to large herbarium collections; checking of ecological notes on labels is frequently disappointing. Also, in literature, exact habitat notes are frequently neglected.

Identifying rheophytes is especially difficult in dry and deforested areas, because in such areas forest has retreated to valleys, as gallery, riverine or riparian forest. Within this riparian forest, there may of course be also other narrow-leaved plants. The main feature distinguishing rheophytes in riparian forest from other narrow-leaved shrubs or treelets is that they (almost) never go beyond the flood level.

As this eco-biological class has in the past not generally been recognized by collectors, the restricted habitat is often not noted by collectors and for this reason it is very difficult to extract data from foreign countries on labels in the herbarium.

As I have been interested in rheophytes since 1928 and have constantly added data to a large file from which I want, if possible, to make a world checklist, I paid particular attention to rheophytes in South Africa in 1975 when I visited riverbeds or rapids. As long ago as 1934, Miss A. A. Obermeijer (now Mrs Mauve) had told me that in South Africa *Gomphostigma virgatum* was a typical rheophyte; this suggested that there could be more examples in that country and this indeed proved true.

Unfortunately I had little opportunity for an intensive study of rheophytes in South Africa: I spotted a few along a small stream near Mt Matsikama in the western Cape, a possible one near the waterfall at Mt Sheba in the north-eastern Transvaal, one near Stellenbosch (Swartboskloof near Jonkershoek) in the south-western Cape and three along the rapids of the Great Usutu River near Mbabane in Swaziland.

It seems desirable to draw the attention of African botanists to this interesting eco-biological class of plants, which must be more numerous in tropical Africa—a region from which there is unfortunately, as yet, little data.

For the present, I have listed the rheophytes of South Africa. In this connection I received valuable information from officers of the Botanical Research Institute in Pretoria.

List of South African rheophytes

ANACARDIACEAE

Rhus montana Diels var. **gerrardii** (Harv. ex Engl.) R. Fernandes.
Shrub 3–4 m. Leaves 3-foliolate, leaflets 3–8 × 0,5–1,5 cm.

Eastern Transvaal, Swaziland, Natal, Lesotho, Transkei, eastern Cape Province.

Along rivers and streams, a distinct riverine shrub, which I found together with *Breonardia* in rapids south of Mbabane (S 24061).

ASCLEPIADACEAE

Kanahia laniflora (Forsk.) R. Br.; cf. Flow. Pl. Afr. t. 900 (1943)

Erect, 0,75–2 m, shrub branching from base, semi-succulent. Leaves narrowly linear-lanceolate, 5–10 cm. Transvaal: Pietersburg, Soutpansberge, Kruger National Park, Pilgrimsrest, Bronkhorstspuit.

Wedged in rocks in riverbeds, covered by flood water for several months in the year; semi-submerged on riverbanks.

COMBRETACEAE

Combretum caffrum (Eckl. & Zeyh.) Kuntze. Syn. *C. salicifolium* E. Mey. ex Hook.

A smallish tree, 1–5 m. Leaves willow-like, 1,25–9 × 0,75–2,50 cm.

Natal (Port Edward), Transkei, eastern Cape Province. Along streambanks and rivers. According to information from Pretoria, it occurs also in hillside bush and some other habitats and is not a strict rheophyte.

COMPOSITAE

Pluchea dioscorides (L.) DC.

Perennial herb or soft shrub up to 3 m. Leaves lanceolate, 3–10 cm × 5–12 mm.

South West Africa (Kaokoveld), Caprivi Strip, northern Botswana, northern and eastern Transvaal, Swaziland, Natal (Zululand coast); also in Zaire, Rhodesia, Tanzania, Mozambique, Kenya and Zambia.

In riverine bush on streambanks, on islands in rivers amongst rocks, or in sandy moist soil in flood beds of rivers; also on sandy flats near rivers.

LOGANIACEAE

Gomphostigma virgatum (L.f.) Baill.; cf. Flora of Southern Africa 26: 169 (1963).

Virgate, slender shrub or herb with woody base, 0,5–2 m high. Leaves 2,5–4 cm × 1–2 mm.

South West Africa, Botswana, Transvaal, Orange Free State, Lesotho, Natal, Transkei, Cape Province.

In riverbeds and on riverbanks, between rocks below high-water level, a characteristic rheophyte.

Nuxia oppositifolia (Hochst.) Benth.; cf. Flora of Southern Africa 26: 153 (1963).

A shrub or slender tree, up to 7 m. Leaves oblanceolate, 3–9 cm × 4–15 mm, faintly dentate or entire.

Transvaal, Swaziland, Natal.

Among boulders along stream courses, occasionally on slopes near rivers, apparently not a strict rheophyte.

MYRTACEAE

Metrosideros angustifolia (L.) J.E. Sm.; cf. Flow. Pl. Afr. t. 1624 (1941).

Shrub 2–4 m high. Leaves smooth, leathery, willow-like 4–7,5 cm × 6–9 mm.

Western Cape Province.

Near or beside mountain streams or river banks of permanently flowing streams. Occurs sometimes also away from streams. I found this in a riverbed on the Gifberg near Mt Matsikama (S 23569).

RUBIACEAE

Breonadia microcephala (Del.) Ridsdale, Blumea 22: 549 (1975) with synonymy. Syn. *Adina microcephala* (Del.) Hiern.

Shrub or small to medium-sized tree, sometimes even a large tree, up to 30 m. Leaves in whorls, crowded towards the twigends, oleander-like, 7,5–25 × 1,5–6 cm.

Widespread, Tchad being the northernmost locality, in Angola, Rhodesia, Mozambique, Malawi, Kenya, Tanzania, northern and eastern Transvaal, Swaziland (Mbabane, S 24059), Natal (Zululand), and in Madagascar.

Gallery forest on riverbanks, rooted in rock crevices, perpetually saturated with streaming freshwater, often partly submerged, in streambeds and along cascades.

SALICACEAE

Salix capensis Thunb.

Shrub to tree up to 10 m high, with drooping branches. Leaves 2,5–7,5 cm by 6–11 mm.

South West Africa, Transvaal, Orange Free State, and widespread in the Cape Province along the Vaal and Orange Rivers.

Riverbanks in brown sandy alluvium, in dry riverbeds and on banks of dams.

S. hirsuta Thunb.

Small tree or bush, up to 4 m high. Leaves hairy, 1,5–3 cm × 5–9 mm.

Cape Province: Olifants R.; Clanwilliam.

Sandy soil of river- and streambanks.

S. mucronata Thunb.

Shrub up to c. 4,5 m. Leaves lanceolate, 1,5–2 cm × 2,5–4 mm.

Cape Province: Olifants R., Breede R., Berg R.

On riverbanks.

The var. *caffra* Burt Davy found on Klipplaat R. and Kei R. grows in similar habitat.

S. subserrata Willd.

A shrub, 1,5–2,5 m high. Leaves lanceolate, 3–6 cm × 8–22 mm. South West Africa (Grootfontein, Kaokoveld) and Botswana: Chobe R.

Riverbanks, near water level.

S. woodii Seem.

Shrub or small tree, 3–4 m high, stem up to 10 cm diameter at base, much branched higher up, not drooping. Leaves lanceolate, shallowly serrate, 5–9 cm × 10–12 mm.

Transvaal, almost all rivers, Swaziland, Natal, Lesotho.

River- and streambanks, in water courses, in clay or sand.

SCROPHULARIACEAE

Bowkeria citrina Thode

Shrub up to 3 m high, usually much-branched. Leaves in whorls of three, 4–6 cm by 8–12 mm.

South-eastern Transvaal and northern Natal.

On riverbanks, often common, sometimes at forest edges.

Freylinia lanceolata (L.f.) G. Don. Syn. *F. oppositifolia* Spin.

Shrub or tree, up to 5 m high, with virgate branches. Leaves willow-like 4–13 cm × 4–13 mm.

Southern Cape Province.

In bush on riverbanks, near waterfalls, in riverbeds, in mountain ravines, also found on the edges of a vlei.

Ixianthes retzioides Benth.

Shrub up to 3 m high. Leaves whorled, very much crowded, linear-lanceolate, with a few teeth towards the apex, up to 6–10 cm × 3–8 mm.

South-western Cape Province.

Riverbanks and in running streams, rooting in the water.

UITTREKSEL

Die bio-ekologiese klas van riofiete, naamlik plantsoorte wat beperk is tot vinnig-vloeiende waterstrome onderkant die vloedvlak, word vir die eerste keer aangeteken vir Suid-Afrika. 'n Voorlopige lys van verteenwoordigende soorte word aangegee.

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