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Phragmites frutescens (Gramineae) re-visited. The discovery of an overlooked, woody grass in Greece, especially Crete

Abstract

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The continuation of studies on *Phragmites frutescens* in Crete revealed its taxonomic distinctness and fairly wide distribution in Crete as well as in Greece in general. A revised morphological description and differentiation against *P. australis* and *P. mauritianus* are presented. As a result, the synonymisation of this tall, woody, branched, winter-flowering reed with *P. australis* is rejected. Its preferred habitats are described as being near permanent water. It is considered to have evolved in isolation from the tropical *P. mauritianus* after post-glacial desertification of northern Africa. By now most stands of *P. frutescens* have been heavily devastated by anthropogenic action.

History of discovery

The incidental encounter with a strange-looking population of *Phragmites* Adans. in NW Crete, Greece, in April 1996, challenged to closer studies in the field and the laboratory, resulting in the description of *P. frutescens* H. Scholz (1996) from several Cretan localities. Prior to its description, three *Phragmites* species were known (Clayton & Renvoize 1986, Watson & Dallwitz 1994): (1) the cosmopolitan and polymorphic *P. australis* (Cav.) Trin. ex Steud. (= *P. communis* Trin., incl. *P. australis* subsp. *altissimus* (Benth.) Clayton and *P. japonicus* Steud.), the common reed, also present in Crete, (2) *P. mauritianus* Kunth, and (3) *P. vallatoria* (L.) Veldkamp (= *P. karka* (Retz.) Steud.), the two latter restricted in their distribution to the Old World tropics. In Africa *P. mauritianus* extends northwards along the Nile river to S Egypt (Cope & Hosni 1991).

Habit differences between the two kinds of reeds present in Crete, *Phragmites australis* and *P. frutescens,* were very impressive in spring 1996 and the plants of the latter incompatible with any published description of *Phragmites* in Europe (Haslam 1972 and references therein, Rodewald-Rudescu 1974, Tutin 1980, Conert 1983): the aerial, up to 6 m tall, straight shoots arise from horizontal or vertical rhizomes, apparently overwinter and persist for several years irrespective of the erratic sexual reproduction on single shoots in a clone. In contrast, in *P. australis* gregarious flowering is a yearly recurrent phenomenon and afterwards the culms die back to

ground level. *P. frutescens* stems tend to be more shrubby in habit, owing to the frequent production of lateral shoots especially on dry soil or in otherwise adverse conditions, when the always sterile and well-branched shoots are densely beset with rigid, sharp-pointed leaves and up to 2 m tall (Fig. 2a). Ramified shoots can be found in *P. australis* too, but only in dwarf and prostrate plants growing on less moist soils (var. *stenophylla* (Boiss.) Bor) are the leaves pungent. Otherwise, (secondary) branching on erect shoots is observed in *P. australis,* e.g., when the main stem is damaged by wind. Some Cretan and especially North African desert plants (Darius 1989; specimens seen) belong here.

During more extensive field work in Crete in 1997-2000, *Phragmites frutescens* plants with well-developed panicles could be observed, not only the stunted and somewhat malformed, "teratological" ones described previously (Scholz 1996). The species proved to be male and female fertile, and widespread near permanent water, especially on swampy places near the sea. It has affinities to *P. mauritianus* rather than *P. australis* as initially supposed. Consequently, the synonymisation of *P. frutescens* and *P. australis* (Chilton & Turland 1997: 102) is rejected. *P. frutescens* is certainly not an aberrant form of *P. australis* (compare Fig. 2-4, Table 1-2).

Relevance of arguments

Features common to *Phragmites frutescens* and *P. mauritianus* can be summarised briefly as follows, using criteria pointed out by Clayton (1970) and Gordon-Gray & Ward (1971) for the latter species: panicles lax; leaf sheaths embracing internodes; both leaf sheaths and blades (laminae) being easily deciduous on older stems, so exposing the culm internodes; leaf blades apically rather stiffly pointed; axillary sterile shoots present (compare Fig. 2a, 2b, 3a).

In contrast, *Phragmites australis* (references as above) is characterised by: more compact panicles; tightly and permanently ensheathed culm internodes; apically softly filiform blades, breaking off from the sheaths; usual lack of any lateral shoots.

The erect, 3-6 m high shoots of *Phragmites frutescens* (at base up to 3 cm in diameter) differ from *P. australis* in a peculiar "phoenicoid" habit (resembling the leaves of the *Phoenix* palm) (see Fig. 2c) due to the patent, rather coarse blades (softer in *P. australis*). Runners (legehalme) could be observed twice (they are said to be absent on *P. mauritianus* (Gordon-Gray & Ward 1971)). Quite exceptional is the very low and erratic or almost totally absent sexual reproduction in *P. frutescens*. The fruiting panicles of four *P. frutescens* populations available are 10-35 cm and the spikelets 7-11 mm long, whereas the fruiting panicles are 15-60 cm and the spikelets 7-16 mm long in *P. mauritianus*. The latter has usually spikelets with more florets and longer callus hairs than *P. frutescens,* whose spikelets are 4-6-flowered and with callus hairs nearly as long as the second lemma. The floral dimensions of *P. australis* considerably exceed those of both *P. mauritianus* (Conert 1961, Clayton 1967, Launert 1971) and *P. frutescens*.

Further distinguishing features of *Phragmites frutescens* are its flowering in winter (November to January) and the surviving of its woody culms after flowering. In Crete, at the beginning of the Mediterranean rainy season in early November 1998, the florest of the spikelets on the panicles just emerged from the uppermost sheaths and had only initials of stamens and ovaries. In May 1999 almost all seed-setting florets were released and dispersed, but the panicled culms were still leafy and green, without any symptoms of dying away. The perennation of the culms may indicate a tropical ancestry of *P. frutescens.* Perennating culms are, in contrast, utmost unusual in *P. australis,* and Haslam (1975), who mentioned populations of *P. australis ("P. communis")* on the Mediterranean island of Malta with culms exceptionally lasting three seasons, therefore suggested their affinity to *P. vallatoria ("P. karka")*. Possibly these populations may belong to *P. frutescens,* too.

Table 1 & 2 summarize the morphological and ecological characters useful for separating the species discussed here. The details given for *Phragmites mauritianus* (Table 1) are based mainly on Gordon-Gray & Ward (1971). As Clayton (1968) emphasised, the *Phragmites* species "cannot be readily separated by any single character". Unreliable characters to differentiate *P. frutescens*

Table 1. Macro-morphological, generative and ecological characters of *Phragmites frutescens, P. mauritianus* and *P. australis* based on Gordon-Gray & Ward (1971) and own observations.

Characters	*P. frutescens*	*P. mauritianus*	*P. australis*
Sterile side branches on erect culms	regularly on mature or post-flowering culms, up to 70 cm long	regularly on mature or post-flowering culms, up to 25 cm long	rare, after damage to the main culm or on dwarfish plants (var. *stenophylla*)
Stems after flowering	dying back only distally (to the next internode below the inflorescence)		dying back totally
Runners (legehalme)	rare	never observed	sporadic
Abscission of mature leaves	leaves totally abscissing		only blades abscissing
Mature culms	woody, up to 3 cm diam., naked, shiny, often suffused with red	woody, often pinkish to purplish	weak, enclosed by leaf sheaths
Leaf blade colour	bluish green	yellowish green	blue-green
Leaf blade tips	pungent		soft (not var. *stenophylla*)
Leaf sheaths	loosely enclosing stem		tightly enclosing stem
Leaves on flowering culms	weakly distichous	blades not or rarely pointing in one direction	blades often directed to one side
Culms on ruderal sites	usually unbranched, leaf blades distichous, culms long; rarely flowering	?	irregulary decumbent to erect, somewhat branched, short; leaves short, somewhat lax; often flowering (= var. *stenophylla*)
Panicles (full flowering)	lax (lower branches without spikelets to the base); branches slightly drooping; panicle usually free	lax; branches strongly drooping; panicle free	dense (lower branches with spikelets to the base); branches erect to scarcely drooping; panicle base often enclosed in uppermost leaf sheath
Horizontal rhizomes	somewhat flattened	terete	somewhat flattened
Flowering time	winter	mainly summer	summer to early autumn
Moisture preference	wetlands with year-round high water supply only	? (sites drier than those of *P. australis*)	widely distributed in wetlands
Soil preferences	loam	sand	sand, loamy sand and mud
Capability of vegetative spreading and survival	high	high	medium

and *P. mauritianus* from *P. australis* are the length of the leaf sheaths (whether or not longer than the internodes), the scabrosity of the blades, the pilosity of the blade collar and the presence or absence of microhairs on the leaf blade epidermis (Gordon-Gray & Ward 1971 for contrasting

Table 2. Size of reproductive structures of *Phragmites* (after Conert 1961, Clayton 1970, Gordon-Gray & Ward 1971, Launert 1971 and original data of Scholz & Böhling); all measurements refer to the length of the structures.

	P. frutescens	*P. mauritianus*	*P. vallatoria*	*P. australis*
Panicles [cm]	(10-)20-35	(15-)30-60	30-60	(3-)10-50
Spikelets [mm]	7-11	7-16	9-12	10-18
Florets per spikelet	4-6	(3-)4-8(-11)	4-6	(3-)4-12
Lower glume [mm]	(2-)3-5	2-4(-6)	3-4	(2-)3-6(-7)
Upper glume [mm]	3-6	3-6	4-6	5-12
Lower lemma [mm]	6-9	(4.7-)6-8(-10)	7-12	(7.5-)9-16
Upper lemma [mm]	4-7	6-11	8.5-11	(7-)9-12
Paleas [mm]	2-3	2-6	2.5-3.5	1.5-4
Callus [mm]	0.5-0.7	0.5-1.5	1-1.5	1-1.5
Callus hairs [mm]	4-5(-6)	4-7	4-7	(6-)8-10
Anthers [mm]	1.2-1.8	1.5-2.25	?	c. 2-4

view). The search for microhairs on *P. frutescens* is very frustrating and on shrubby plants often in vain, but could be successfully accomplished. Only once on Cretan *P. australis* were microhairs seen, thus not confirming contrary previous statements from 1960 onwards (Metcalfe 1960) for this species.

Material of *Phragmites frutescens,* cultivated outdoors in a water-filled trough at the Botanic Garden Berlin-Dahlem, developed from early summer 1999 until end of August 1999 a young, basally woody culm up to 1 m tall, up to 2 cm in diameter and with sprouting axillary buds. In mid October 1999 already up to 35 cm long branches developed along the 2 m tall main culm. Older culms increasingly branched, when somewhat bent (Fig. 4b). On 12 November the aerial parts were killed by low frost (-5 °C).

Fig. 4c shows "normal" *P. australis* grown under the same conditions. The plant, however, was raised from a typical individual of the dwarfish and pungent var. *stenophylla* (voucher at B: Crete, Karteros, E Iraklio, coastal sands, 25.10.1997, *Böhling & Greuter 6974*). This proves that, in contrast to *P. frutescens,* the particular morphology of *P. australis* var. *stenophylla* is a mere response to environmental factors, lost under more suitable conditions and therefore taxonomically of no value.

Why so long undetected?

Tall grasses such as the woody bamboos, the giant reed (*Arundo donax* L.) and *Phragmites* species (to 10 m tall culms!) are difficult to collect and preserve for taxonomic studies. *Phragmites* taxonomy is further impeded by high environmentally induced plasticity, suspected introgressive hybridization and a lack of any correlation of chromosome numbers (2n = 48 to c. 264; see Connor & al. 1998 and Clevering & Lissner 1999) with morphological features in *P. australis*. However, the main cause that *P. frutescens* escaped the attention of botanists so long, is its rare, very erratic and late flowering. It may well be assumed that any sterile *Phragmites* population has been regarded as belonging to *P. australis* or, perhaps, *Arundo* or *Arundo* hybrids. Finally: when generations of botanists have agreed on the view that only one, admittedly variable species, *P. australis,* is present in Europe, the silent supposition is that they could not be wrong. The long

history of botanical exploration in Europe and its results (for Crete see Turland & al. 1993, Chilton & Turland 1997) seem to provide strong evidence and support.

To save the doctrine of a monospecies genus *Phragmites* in Europe it could be argued that *P. frutescens* has been introduced or has invaded recently. In Crete (and elsewhere) the coastal plains have suffered severely from human activity. The long-established artificial drainage of primary *Phragmites* swamps resulted in conversion to pasture land, nowadays largely replaced by buildings of tourist and traffic centres, roads and public places with planted trees, and by waste land. It appears very unlikely that *P. frutescens* is a naturalized recent introduction, when we consider its occurrence in suitable habitats nearly everywhere on the island, as well as in the southern Aegean and Greece as far as studied. *P. frutescens* resists extinction in now fragmented, drained swamps and is declining increasingly. This shows its residual character, not an invading behavior. Its indigenous occurrence on the other hand would not be surprising in the light of the investigations of Gradstein & Smittenberg (1977) and Yannitsaros & Koumpli-Savantzi (1991), which revealed the richness of the hydrophilous element in the Cretan flora.

Evolution from a relic of tropical origin?

The present working hypothesis for the evolutionary history of *Phragmites frutescens* is the following: *P. frutescens* differentiated from *P. mauritianus,* which in former (pluvial) times covered a ± continuous area from regions of the equatorial belt to territories in the north. The desertification, in North Africa beginning c. 8000 a BP (Pachur & Altmann 1997), subsequently left northern populations of *P. mauritianus* in isolation. Many of them vanished, other survived, adapting to climatic changes and giving rise to *P. frutescens*.

It is remarkable how far away it is now from its tropical ancestor as regards its flowering time. In contrast to what would be expected from a plant of tropical origin, it is flowering and seed-setting in winter.

Ecology and distribution

Phragmites frutescens is found in remnants of originally extended, continuous populations along waters which are perennial over long periods. It occurs typically in coastal alluvial plains where rivers, karstic springs or groundwater streams originating in a mountainuous hinterland rich in water ensure sufficient water supply all the year round. Here it inhabits some of the moistest, waterlogged sites.

On Crete the species is missing in the east and most of the south (Fig. 1), probably because lower precipitation, geology and steep relief do not allow the existence of larger streams or other habitats with a sufficient water supply. It is obviously widespread in the coastal alluvial flats of NW Crete near groundwater level, in the Messara plain S of Iraklion, which is well supplied with water, and in the littoral alluvial plain W of Iraklion supplied by a strong karstic spring. The most undisturbed Cretan stand is found at the river Akoumianos, SW of Spili, but low water level (only during the last comparatively dry years?) prohibits vigorous growth. *P. australis* is missing at the mouth of this river.

The only other known locality of *P. frutescens* in the S Aegean is on Rhodes. There, remnants of vast populations are found at the mouth of the river running through the unique Petaloudes ("butterfly") valley with its luxuriant *Liquidambar orientalis* riparian woods. The estuary has been cultivated in the recent past to provide ground for the electric power station of the island.

Additional observations revealed: in the Peloponnisos and Sterea Hellas *P. frutescens* seems widespread too, preferring estuaries of rivers bearing a lot of water. One specimen is from the Cyclades (Naxos). It is also widespread in the coastal alluvial plains of the northern Greek Sithonia peninsula (Chalkidiki), where a good water supply exists from rivers originating in the siliceous mountains as well as some protection from cold north winds. The great alluvial plains of the Aliakmon river W of Thessaloniki, extending along the Vardar valley, seem to provide in-

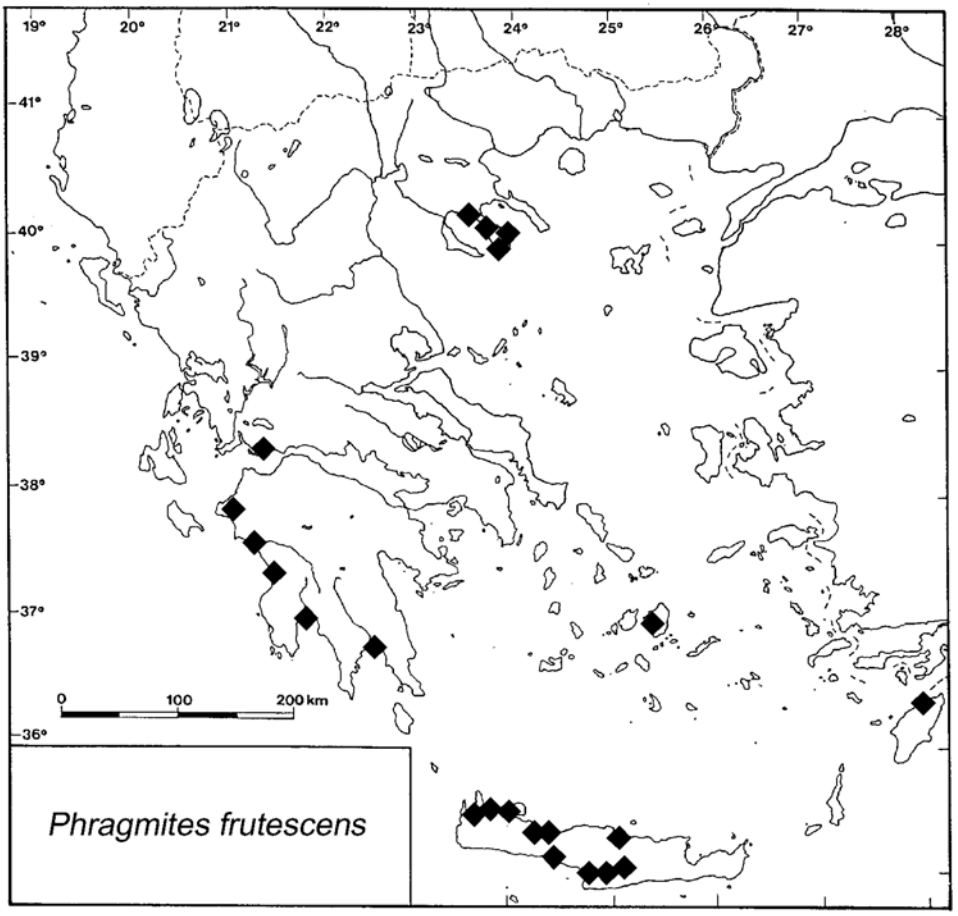

Fig. 1. *Phragmites frutescens* – known distribution in Greece.

sufficient protection from cold winds, because *P. frutescens* is totally replaced by extended stands of *P. australis*. Two recent collections (sterile plants, vouchers at B) from Syria and Israel belong to the new *Phragmites* species too.

Quite high warmth demands are possibly reflected in its irregular, late flowering. According to the temperature summation rule, not every year might be warm enough to enable flowering and fructification. Favourable conditions for generative reproduction possibly occur only in "hot" years, especially those with warm spring and winter, sufficient water supply provided. Other eco-factors influencing the stands of *P. frutescens* are strong winds breaking the culms and sea-spray drying out the leaves.

On Crete, a remnant of an undisturbed, natural, well developed stand has been studied in detail: it is a c. 100 m² large, wet hollow on sandy loam (20 % clay, 22 % silt, 58 % sand; low to medium nitrogen, phosphorus and potassium levels) just E of Neos Kournas, situated between the sea and the karstic spring lake of Kournas, the only perennial, natural lake of Crete. The wet centre is inhabited by pure *P. frutescens,* growing up to 6 m, but with only a few (10) developed inflorescences in November 1998 (Fig. 3b). With reduced moisture the reed was followed by *Calystegia sepium, Dorycnium rectum*, then by *Cirsium creticum, Epilobium parviflorum, Apium nodiflorum, Cyperus longus* s.l., *Galium debile, Carex otrubae, Pulicaria dysenterica, Lathyrus*

annuus, Oenanthe pimpinelloides, Typha domingensis, Rubus sanctus, Poa trivials subsp. *sylvicola, Potentilla reptans, Panicum repens*, *Lythrum junceum, Myrtus communis, Rumex conglomeratus, Scirpoides holoschoenus, Ranunculus muricatus, Plantago major* and *Dittrichia viscosa,* at the last by *Arundo donax*. *P. australis* is entirely absent. In neighbouring, open communities on a similar substrate *Alisma lanceolatum* and *Bromus arvensis* (here recorded for the first time from the S Aegean) occur. It was said that this stand of *P. frutescens* was burned regularly in the past because it produces impenetrable thickets. The latter is really true, if no device such as a machete or saw is available. Like the culms of *Arundo donax,* those of *P. frutescens* could be used for building, pipe instruments, walking sticks or fishing rods.

Another (semi-)natural site with *Phragmites frutescens* is situated N of Asprouliani on superficially dry coastal sands (sand fraction > 94 %, very low nitrogen, phosphorus and potassium levels), formerly probably cultivated. Here, the reed is associated with *Bromus diandrus, B. rigidus, Vulpia fasciculata, Lagurus ovatus, Centranthus calcitrapae, Erodium laciniatum, Euphorbia terracina, Papaver rhoeas, Rumex bucephalophorus* subsp. *bucephalophorus, Silene colorata, Sixalix atropurpurea* subsp. *maritima* and *Trifolium campestre*. All the reed plants were sterile, the shoots only 1-3 m tall and xeromorph, showing, if not branched, the characteristic phoenicoid form.

Phragmites frutescens flowers rarely, if at all, even on what seem to be luxurious sites. In contrast, the ability to regenerate after disturbance (ploughing, siltation or partial covering with soil and waste) is much more effective in *P. frutescens* than in *P. australis*. Often, the two reeds grow sympatrically with *Arundo* spp., the latter on the drier places, *P. australis* on the wetter places and *P. frutescens* in intermediate situations.

The sylleptic and next-year(s)-branching of the culms (Fig. 2a), the "phoenicoid" habit of unbranched shoots (Fig. 2c, 3c, 4a-b) and the abscission of the leaves (Fig. 2a, b) are the most practical features to recognise *Phragmites frutescens* in the field, when found sterile and xeromorphic on the remaining, mostly ruderal or degraded sites.

A list of specimens and localities, including further ecological data, of *Phragmites frutescens* supplementary to Scholz (1996: 522) is provided at http://www.bgbm.fu-berlin.de/bgbm/library/publikat/willd30/scholz&boehling.htm.

Phragmites frutescens – soon extinct?

As a plant of wet alluvial plains, supplying the best arable land after drainage, most of the stands have been destroyed by now. Small remnants of swamps are used for waste disposal or are influenced by continuous drainage. Especially those near the coast are filled to change these "useless" places into touristic or industrial areas. For example, in the vicinity of hotels swamps are disliked as breeding places of mosquitos, and on Rhodos the pristine stands have been replaced by an electric power station. It is time to conserve and regenerate wetlands along the coasts, not just for *Phragmites frutescens* but for the great variety of hydrophilous plants and animals.

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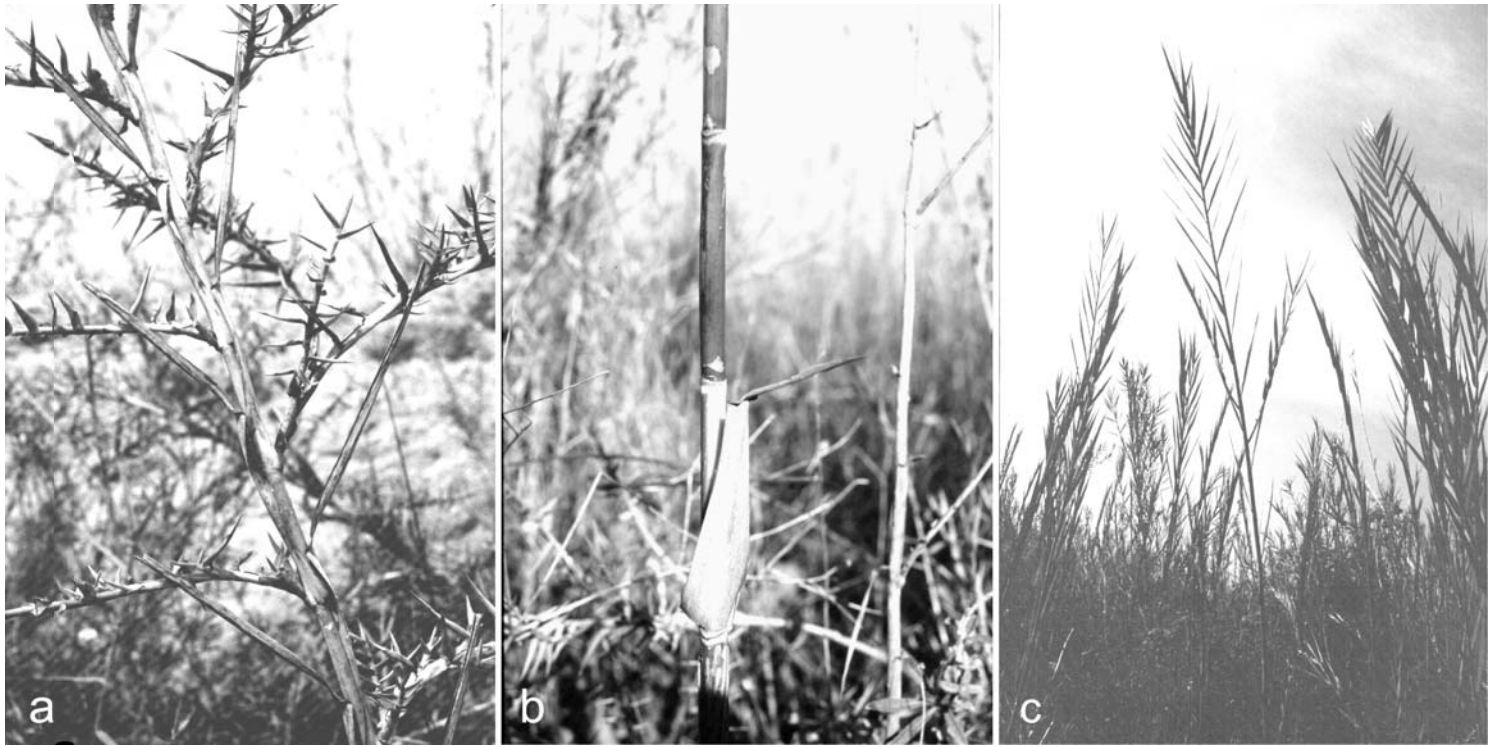

Fig. 2. *Phragmites frutescens* – a: mature main stem with sterile side branches, loose leaf sheaths and totally abscissing leaves; b: mature stem being naked (after natural abscission of mature lower leaves), shiny, suffused with red, woody; c: phoenicoid shoots, grown up to c. 4 m tall culms with 3 cm diameter at base (in first season!), partly with sylleptic branching. – Photographs by N. Böhling, a: Greece, Crete, Asprouliani, 16.4.1998, b: ibid., 9.11.1998, c: Greece, Chalkidiki, Sithonia peninsula, between Neas Marmaras and Lagomandra, 20.9.1999.

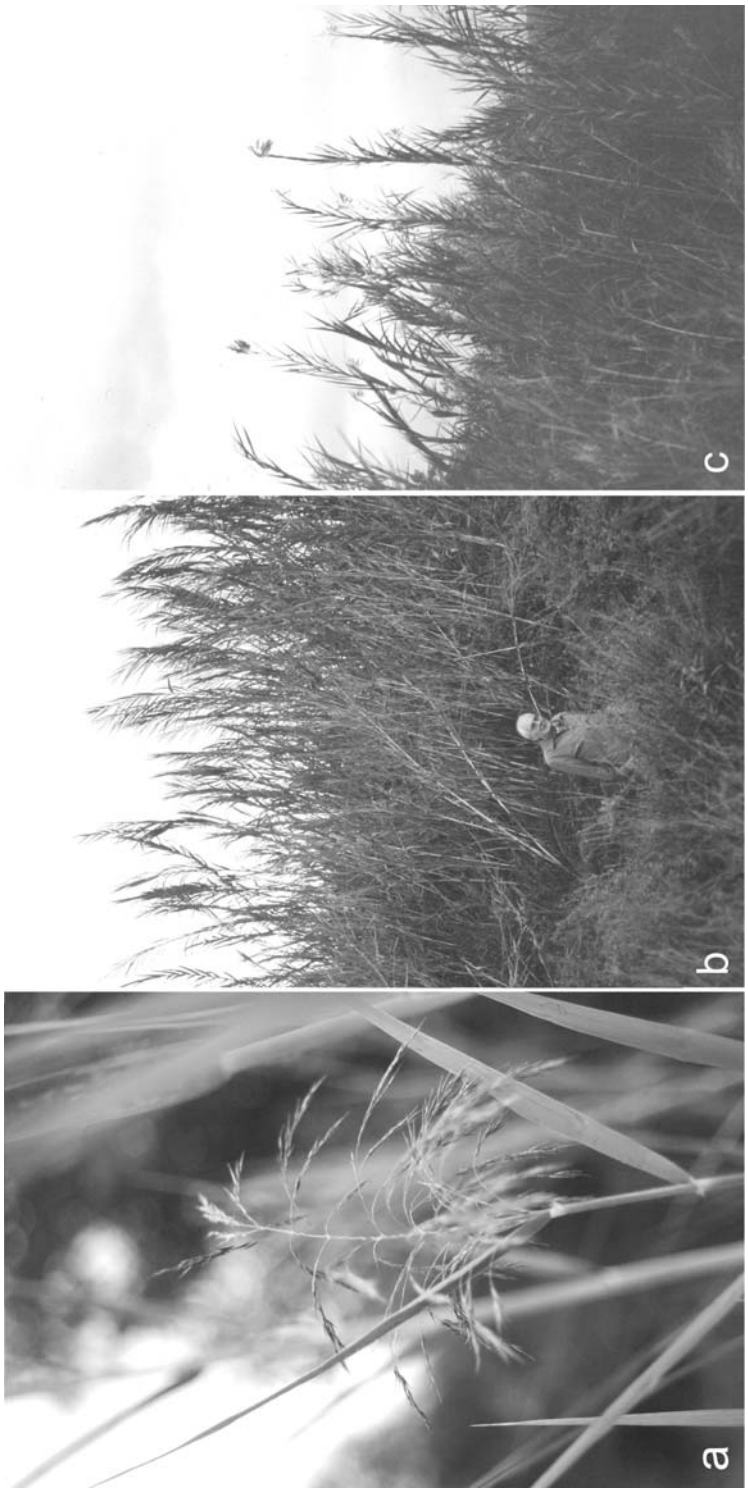

Fig. 3. *Phragmites frutescens* – a: young, lax, c. 15 cm long panicle with scarcely drooping branches, leaves erect, long-attenuate, pungent; b: stand up to 6 m tall with woody stems to 2 cm in diameter, forming dense, impenetrable thickets on waterlogged clayey soil; c: flowering is a rare event, only to c. 10 % of the culms produce panicles, which clearly overtop the reed. – Photographs by N. Böhling, a: Greece, Crete, Gerani, 12.11.1998, b: Crete, Neos Kournas, 9.11.1998, c: Crete, Kolimbari, 3.1.2000.

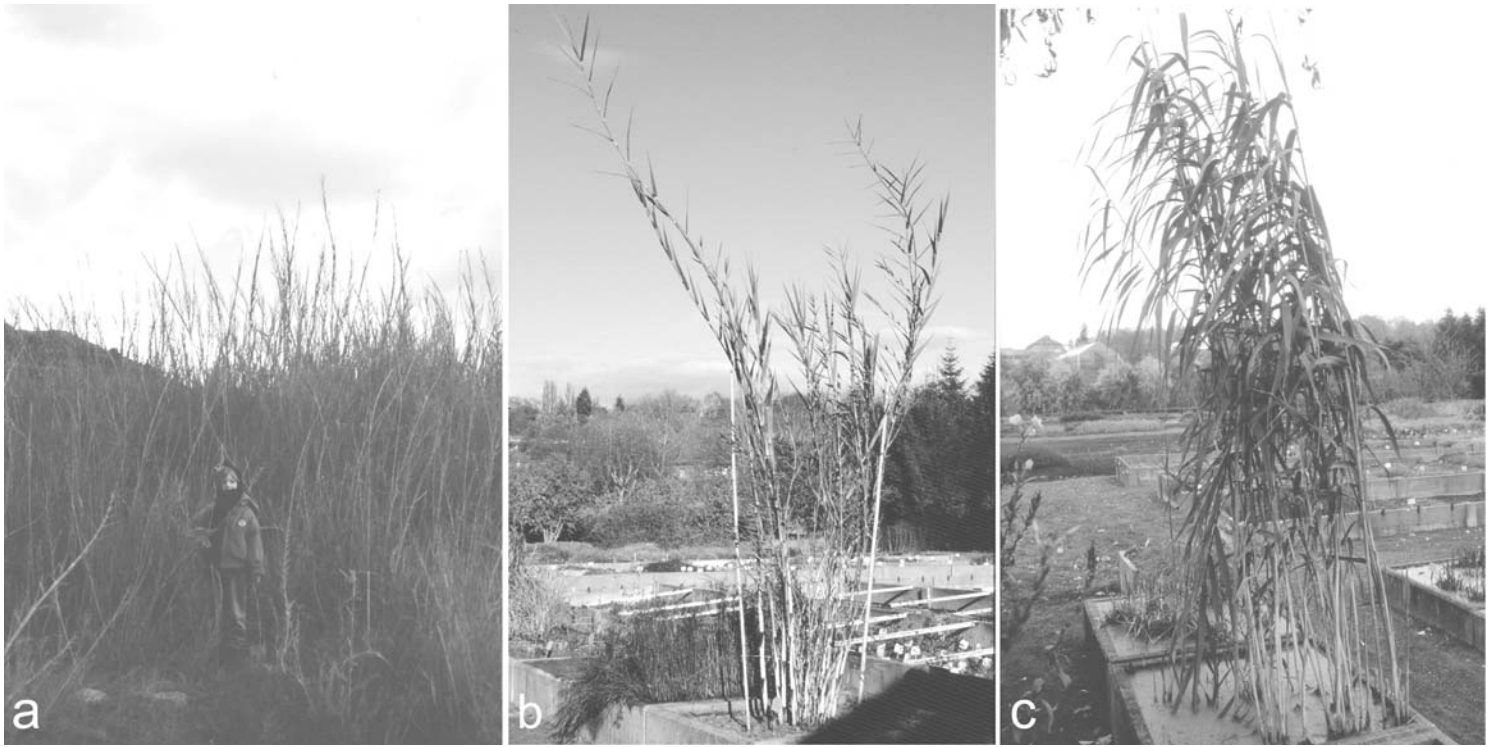

Fig. 4. *Phragmites frutescens* (a-b) and *P. australis* (c) – a: stand with xeromorphic aerial shoots, on a dryer site in Crete, Saktouria, mouth of Akoumianos river; b: cultivated in the BG Berlin-Dahlem, culms c. 5 months old, originating from Crete, Neos Kournas, 9.11.1998, *Böhling & Scholz 9209* (voucher at B); c: *P. australis* ("var. *stenophylla*") cultivated in the BG Berlin-Dahlem, culms c. 5 months old, soft blades mostly directed to one side, originating from Crete, E Iraklio, Karteros, 25.10.1997, *Böhling & Greuter 6974* (voucher at B). – Photographs by N. Böhling (a: 5.1.2000) and I. Haas (b + c: 11.11.1999).