Short communication

Studies in Cyperaceae in southern Africa 42: Pseudo-vivipary in South African Cyperaceae

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Abstract

An account is given of pseudo-vivipary (vegetative apomixis) in South African Cyperaceae. Taxa exhibiting this reproductive strategy are tabled. Stress that effects plant population deterioration and eventual non-survival is attributed as causative; in particular water stress, either as maintained inundation or undue depletion. Habitat conditions appear to govern the balance between fruiting and pseudo-vivipary. This balance is changeable from season to season, area to area, species to species and within species. The viability of seeds within fruits formed upon inflorescences that also are in part pseudo-viviparous has not been tested.

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1. Introduction

The family Cyperaceae (sedges) includes short-lived and longer-lived perennials as well as annuals. In South Africa, the annuals are mostly plants of the sandy alluvium along water-courses in warmer parts of the country and in dune slacks in dry areas such as the Kalahari. Some are present in shallow, poor soils on rock outcrops on hilltops where there may be soil water seepages maintained by dews and occasional rain, with temperature extremes somewhat mitigated by the rocks themselves.

The perennials are generally in stands in permanently or periodically wet or damp situations where inundation including occasional intensive flooding is likely. Many are taller and more robust than the annuals; they are often elaminate with inflorescence bracts elongated to provide greater photosynthetic surface. Where stands of these elaminate species extend into land adjacent to permanent water the plants flourish less well, and if affected by disturbance such as fire, or defoliation like cropping by indigenous or feral animals, or artificial mowing, tend to produce leaf blades (Baijnath, 1973; pers. obs. KGG).

Little is known with certainty of the reproductive capacities of sedges. All produce one-seeded fruits frequently termed “achenes”, but more accurately interpreted as “nutlets”. Fruit production by the annuals may be prolific, leading, under rather specialized conditions, to their wide distribution as weeds, for example Cyperus difformis L. “rice weed”. With few exceptions these fruits are very small, light in weight and distributed by water, wind and animal vectors, especially birds. The perennials, in general, produce fewer fruits, sometimes none that contain viable seed. These are mostly larger, heavier and more elaborate than those of the annuals, for example species of Scleria P.J. Bergius and Bolboschoenus (Asch.) Palla. Among the genera overall, features suggest there has been specialization for distribution. There are heavy fruits that sink in water to await germination under favourable conditions for growth of the seedlings (for example some Bolboschoenus and some Scleria species); others with inflated cells that aid in flotation (for example some Bolboschoenus and some Schoenoplectus (Rchb.) Palla spp.); yet others in which the pericarp is soft and corky (for example plants that are usually submersed,
namely those of *Cyperus pectinatus* Vahl and *Oxyacrum cubense* (Poesp. & Kunth) Lye).

Little is known of germination requirements such as periods of dormancy, embryo viability and seed bank reserves — virtually nothing of South African species! These criteria all have significance in the maintenance and/or re-establishment of natural stands of species that are dependent upon the availability and condition of their required habitats. Embryo structure has been given taxonomic importance, especially by the work of Van der Veken (1965), who established that embryo structure differed in detail among the genera at the time of fruit dissemination. Some embryos are at an early stage of development at the time of fruit dispersal (for example *Rhynchospora* Vahl spp.), which ensures a period of dormancy before germination. These embryo differences have been relied upon to strengthen and add to knowledge of generic limits within Cyperaceae — an aspect of the family that is controversial and still undergoing study. What does remain to be achieved is for this embryo information to be correlated with germination studies, especially for South African taxa.

However, among the perennials, it is doubtful if fruit production is always the prime reproductive method. The plants are mainly rhizomatous, and growing as they so often do along water lines where periodic inundation and flooding are fairly regular occurrences, distribution and regeneration (re-establishment) by vegetative organs (fragments) is significant in maintaining and increasing stands. Such vegetative propagation of course disallows the variation from generation to generation that is so important a feature of sexuality. Two other less obvious reproductive strategies operate within Cyperaceae.

The first is amphicarpy, the production of aerial and basal fruits on single plants. South African species known to exhibit this strategy are *Bulbosystis humilis* (Kunth) C.B. Clarke, *Schoenoplectus erectus* (Poir.) J. Raynal subsp. *raynali* (Schuyler) Lye and *Triopnptcles solitaria* (C.B. Clarke) Levyns. These are mostly annuals or short-lived perennials of dry situations where water is periodic (rainfall) and vegetation sparse. Differences between aerial and basal nutlets as effective reproductive units have not been investigated. Fire has been suggested as a causative factor of amphicarpy in upland species and seasonal flooding that removes aerial fruits as possibly selective in wetland examples (Leck and Schütz, 2005). Amphicarpy has been more fully studied in South African taxa (Browning, 1992; Bruhl, 1994) than has pseudo-vivipary, the second less obvious reproductive strategy.

Pseudo-vivipary is also known as vegetative apomixis. It is the production on the parent plant of adventitious buds that are capable of development into new individuals (ramets of a clone) in association with floret production in inflorescences. True vivipary, namely the germination of an embryo with penetration of the pericarp while still attached to the parent plant, is unknown in Cyperaceae. Elmqvist and Cox (1996) did not record the occurrence of pseudo-vivipary in Cyperaceae, probably because it was suspected of being induced by attack by systemic parasitic fungi. However the strategy had been documented in *Eleocharis vivipara* as early as 1929 (Svenson, 1929, cited by Miao et al., 1998) and at least 15 South African sedges are known to be pseudo-viviparous.

The purpose of this paper is to list the South African sedges known to exhibit pseudo-vivipary: to summarize what is known of the phenomenon in relation to the species that display it, and to emphasize its importance as a means of propagation in habitats that constantly fluctuate and are uncertain, and therefore stressful to plant survival.

2. Results and discussion

As far as has been determined, all pseudo-viviparous South African sedge taxa (Table 1) are long- or short-lived perennial hydrophytes or helophytes. Their tolerances to water stress and its consequences and to shading out by competing vegetation differ from species to species. But, in general, these adverse habitat conditions are deleterious to population survival and stimulate pseudo-vivipary, which is a strategy to hasten propagation under adverse environmental conditions. The adventitious buds arise from lateral meristematic tissue in the axils of inflorescence branches, bracts, or floral scales (glumes) of spikelets; from inflorescence branch apices; or, far less often, from the axils of scale leaves of rhizomes as bulbils. Such bulbils are usually not considered evidence of pseudo-vivipary.

The trigger(s) that activate this plantlet growth are uncertain. Predoming evidence suggests “inundation stress” as mainly causative (Leck and Schütz, 2005), but what this term implies is not always precisely defined. Its most likely interpretation is surely of rising water levels that are maintained until lower parts of some of the culms decay, causing the inflorescences they carry to bend to water level, so immersing some of the inflorescence branches. This lateral positioning that gives contact with either water or soil activates further plantlet growth. Alternatively, lowered water levels that are maintained may result in decreased water flow, resulting in reduced available oxygen and eventual stagnation. Both sets of conditions have been reported as activating pseudo-vivipary in *Cyperus prolifer* Lam. (Bajnath, 1973; Bajnath and Getliffe, 1977) (Fig. 1). This is the species that has been most thoroughly investigated in South Africa and for detailed information

<table>
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<th>Table 1</th>
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<td>List of South African species of Cyperaceae known to reproduce by pseudo-vivipary</td>
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<th>Species</th>
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<tr>
<td><em>Chladium mariscus</em> (L.) Pohl subsp. jamaicense (Crantz) Kük.</td>
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<td><em>Cyperus involucratus</em> Roth.; <em>C. sexangularis</em> Nees; <em>C. testilis</em> Thunb.</td>
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<td><em>C. marginatus</em> Thunb.</td>
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<td><em>C. prolifer</em> Lam.; <em>C. x turbaria</em> Bajnath</td>
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<td><em>C. sphaeroespermus</em> Schrad.</td>
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<td><em>Eleocharis limosa</em> (Schrad.) Schultes</td>
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<td><em>I. pellucola</em> B.L. Burt</td>
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<td><em>I. prolifer</em> (Roth.) R. Br.</td>
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<td><em>Kyllinga pauciflora</em> Ridley</td>
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<tr>
<td><em>Scirpoides spinulifer</em> (Schrad.) Sojak</td>
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Species that are closely related morphologically, and therefore often confused, are placed together.
readers are referred to the references above. Other species exhibiting pseudo-vivipary are discussed below.

*Cladium mariscus* (L.) Pohl subsp. *jamaicense* (Crantz) Kük. has become much reduced in number and extent of stands in wetlands along the eastern coastline south of St Lucia Estuary, due probably to the increasing demands of agriculture and population expansion. Some inflorescences produce many strong plantlets (Fig. 2). *Cladium jamaicense* (sic) “sawgrass” in the Florida Everglades (a sub-tropical wetland) is reported as exhibiting pseudo-vivipary (Miao et al., 1998). The South African entity was distinguished from the Florida entity by Kükenthal (1942) on possessing characters of both *C. mariscus* (spikelet size and anther connective prolonged) and *C. jamaicense* (fruit size and shape).

*Cyperus involucratus* Rothb. has become a favoured garden subject (now naturalized world-wide). In its indigenous stands along rivers and streamlets in eastern southern Africa where it is prolific, water is usually plentiful and adventitious plantlets on inflorescences are not always present. This variation has also been observed under cultivation. Clones from a number of indigenous populations transplanted into a Durban garden (by CJW), and grown on under approximately uniform habitat conditions for several years, have varied in the extent of pseudo-vivipary shown from season to season; sometimes showing no evidence of it, or with few plantlets developed only late in the season. In this species the inflorescence terminates the culm and consists of a series of leaf-like bracts separated by very short internodes. Each bract subtends latent axillary meristematic tissue from which, at flowering, an inflorescence shorter than the bract develops. In the pseudo-viviparous inflorescences in some, but only in some, of the axils a vegetative shoot forms above the inflorescence. This shoot may multiply to form one to three closely placed additional shoots that soon swell basally. Most of these plantlets rapidly produce a slender elongate peduncle bearing a miniature, perfect or imperfect, inflorescence (Fig. 3). As they age the main culms of the plant, some heavy with plantlets, incline until prostrate on the substrate or supported by surrounding vegetation. When at substrate level, either in water or on soil, the plantlets are stimulated to produce adventitious roots and further growth, thus achieving asexual replication. It would seem that it may be not only “water stress,” whether too much or too little, that is the trigger to plantlet development; since only some clones and some meristems within an inflorescence exhibit pseudo-vivipary, there may operate some further (genetic?) control not yet determined.

*Cyperus marginatus* Thunb. has a very wide distribution in sub-Saharan Africa. It occurs along water lines from east to west of the subcontinent and northwards into tropical Africa. In South Africa three elements are detectable within the species.
The eastern expression is helophytic, fringing water lines especially at higher altitudes. Here water levels alter marginally from season to season, but water is always in sufficient supply; flooding may be occasional, but is always briefly maintained because of good drainage. In this expression pseudo-vivipary is unknown. On the central plateau, where plants again follow water lines, but are often isolated on the drying margins of pools, adventitious plantlets are occasional on inflorescences. Into the western sector (Northern Cape, Namibia, Angola), where the species yet again closely follows water lines and is especially associated with springs (fountains — hence a synonym *C. fonticola* Kunth), pseudo-vivipary is exceedingly well developed (Fig. 4). Under these semi-desertic conditions periodic flash flooding with inundation takes place; but lengthy periods of uncertain, often inadequate, water supply are far more frequent. It is not known which set of conditions activates plantlet growth; probably both are stimulatory. Culms of these plants often elongate considerably during growth and with the weight of developing plantlets from the apical inflorescences, incline to become prostrate on the substrate where rooting of the plantlets commences. In this way the culms, which far exceed the underground rhizomes in length, take on the function of spatial dispersal, keeping mostly to the line of available water. One of us (C.J. Ward 13713 NU) recorded a prostrate culm 3.5 m in length.

Leck and Schütz (2005) cite A.E. Schuyler (pers. comm.) as believing that in American species of *Scirpus* L. the elongated culms take on the function of stolons by increasing vegetative propagation spatially. Genus *Scirpus* is not represented in South Africa. Somewhat similar species are included within *Schoenoplectus*.

Browning (1991) considered pseudo-vivipary in an extensive study of *Schoenoplectus corymbosus* (Roem. & Schult.) J. Raynal and *S. brachyceras* (A. Rich.) Lye. These two species are very closely allied morphologically and in habitat. Haines and Lye (1983) interpreted them as varieties, stating that var. *corymbosus* did not develop adventitious plantlets, while var. *brachyceras* did. For South Africa, Browning found pseudo-vivipary in both species. Collectors, especially in the Okavango swamps, Botswana, have made frequent reference to culms...
bearing plantlets that are bent or are dipped in water. Our study suggests it is not inundation that triggers plantlet growth, but rather the habitat conditions that precede it. Any habitat stress may be causative. Higher water levels accompanied by decreased water flow may bring about decay of the basal parts of culms so that bending or inundation results. This quickens plantlet growth already initiated by the stimulus of unfavourable habitat conditions. Alternatively, decreased levels leading to stagnation may also be causative.

The South African species of *Cyperus* and *Schoenoplectus* that are known to be pseudo-viviparous mostly have elongate, nodeless culms and grow most favourably in permanent moving oxygenated water. *Cyperus sphaerospermus* Schrad. differs in that it is branched, leafy and “scrambles” among grasses and other plants along streamlets and in seeps where water is either in plenty over short periods, or sparse but not wanting for much longer spells. This species proliferates extensively by pseudo-vivipary, plantlets being developed from the axils of one or both of the elongate inflorescence bracts (Fig. 5). However, this does not prevent spikelet formation, which, during the early growing season, may be prolific. Some of the florets appear perfect and contain ovaries that reach fruiting size; whether such ovaries contain perfected embryos has not been determined. As the season advances and habitat conditions become less favourable, plantlets increase. This is based on field observation and no statistics have been recorded. This needs to be done. *C. sphaerospermus* makes an excellent starting point as it is profuse and widely distributed in eastern South Africa.

The rare and poorly known *Kyllinga pauciflora* Ridley is somewhat like *C. sphaerospermus* in general facies and habitat. It is often pseudo-viviparous (Getliffe, 1964). Its few florets per spikelet; its close morphological similarity with the far more widespread and profuse *Kyllinga erecta* Schumach. and its limited distribution on the outskirts of stands of that species suggest a definite possibility of pseudo-vivipary in conjunction with hybridisation. Grant (1971) pointed out that pseudo-vivipary is often combined with natural hybridisation, which frequently involves a degree of genetic imbalance that disturbs normal sexual reproduction. This should be considered as perhaps additionally causative in this species.

The genus *Isolepis* R. Br. is now regarded as close kin to *Cyperus* L. (Muasya and Simpson, 2002). Its components are mostly low-growing, soft textured helophytes, either erect, or with culms immersed in shallow water swaying gently with the flow, or populating recently deposited alluvium, where there is
little or no competition from existing vegetation. *I. prolificra* (Rothb.) R. Br. is a good example of a pioneer populating open alluvium; this is done by means of slender, elongated, soft culms terminating in small inflorescences and carrying plantlets that have already begun growth, having received photosynthetic products from a parent (Fig. 6). The weight of the inflorescence brings about inclination of the culm to substrate level, some distance from the parent, where rooting and further growth takes place. Thus coverage is far more rapid and more certain than by fruit distribution, germination and seedling establishment. Rapid establishment is important in habitats where water levels are consistently uncertain. *I. costata* A. Rich. develops many proliferating inflorescences in shallow water. Presumably some of the plantlets float away and regenerate at a distance. Spikelets with fully formed florets often accompany plantlets. In our experience the ovaries, with pericarp characteristically marked by longitudinal striations (lines of cells), do not contain seeds and so are non-propagative — an expenditure of unproductive material in an uncertain habitat!

*Eleocharis* R. Br. species also exhibit pseudo-vivipary. In South Africa *E. limosa* (Schrad.) Schult. proliferates profusely by this method (Fig. 7). Most inflorescences develop a plantlet from the axil of the lowest bract while floral scales each carry a floret, usually with a fully formed ovary. Again, nothing is known of the viability of the embryos within the seeds of these fruits. *E. dreyeana* Steud. is also often frequent in slowly flowing, shallow water. Its inflorescences are not known to proliferate, perhaps due to its slightly different habitat preference. Its plants are more deeply rooted in more permanent water, than are those of *E. limosa*. There are other species within *Eleocharis*, *Isolepis*, *Cyperus* and tentatively *Tetaria* that have been reported as occasionally pseudo-viviparous. But we have no direct evidence by which to confirm these intimations.

3. Conclusions

Further study is needed of this rather poorly known method of vegetative propagation, particularly regarding its causes and long term effects. Most information has been obtained from field observation of natural stands. From our studies we conclude:

In South Africa pseudo-vivipary is known only for sedges associated with water, particularly water lines where levels are fluctuating from periods of insignificant change to spells of inundation or excessively low water. Any sets of irregular habitat conditions may influence the balance between fruiting and pseudo-vivipary, which latter is a means of asexual reproduction that operates when population survival is endangered. In some cases it results in the rapid colonization of bare or scantily vegetated areas where seedling survival may be doubtfull and very much slower, as plantlets benefit from photosynthetic products derived from parental individuals and are thus advanced beyond seedlings.

Pseudo-vivipary does not contribute to seedbank establishment, as it reduces viable seed production. Therefore it is valuable in the short term when habitat and climate merely fluctuate. However it may be disadvantageous by limiting the variability engendered by sexual reproduction that offers the possibility of adaptation to more permanent long term environmental change.

“Water stress” is presently regarded as causative. Our observations have revealed that in one species at least (*C. involucratus*), not all clones exhibit pseudo-vivipary in a single season; nor do all axillary meristems within a pseudo-viviparous inflorescence develop plantlets. This is suggestive of some control in addition to habitat conditions.

In Cyperaceae pseudo-vivipary comes about by the development of a plantlet adjacent to (usually above) an inflorescence or a floret within a spikelet. This differs from development in Poaceae where “... the most familiar situation is the conversion of the whole spikelet or part of the spikelet into a leafy shoot” (Vega and de Agrasar, 2006).

Expressed in its simplest terms, pseudo-vivipary in South African sedges is a return to vegetative growth following flowering. It is nothing to do with vivipary. It is the close association of a vegetative shoot with a fruit that has occasioned this term’s application to this phenomenon. It has not been reported for annuals, only for perennials that are long- or short-lived.

Acknowledgement

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References


Fig. 7. *Eleocharis limosa* (Schrad.) Schult. Pseudo-viviparous inflorescences on plant from banks of drain in reed swamp. Richard’s Bay, KwaZulu-Natal. C.J. Ward 8697 (NU). Scale bar: 2 cm.


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