Ludwigia palustris (L.) Ell. in England with special reference to its dispersal and germination

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ABSTRACT

Data are furnished respecting the seed-production and germination of *Ludwigia palustris* (L.) Ell. Its occurrence in England is discussed and the handicaps to its dispersal emphasised.

Ludwigia palustris was first recorded for Britain in 1666 (Raven 1963) and R. Sweet noted it as introduced here in 1776 (Sweet 1827). Borrer found it near Brockenhurst, Hants., in 1843: E. T. Bennet recorded it again in a nearby ditch after an interval of nine years. This area was subsequently searched in vain until, no less than 26 years later, the species was once more discovered there by Bolton King. After a further period of 91 years, I myself found it near Brockenhurst in 1969, in an area repeatedly searched during the previous decade. In another locality, some four miles from Brockenhurst, the species has been present in in some quantity over a period of years; so reappearance near Brockenhurst might be due to bird transport or to the effect of the very dry autumnal spell of 1969 upon seed dormant in the mud that then became exposed to air and light. For a period of some years at least this area had been under water, so either source of origin is not improbable.

In various continental Floras *Ludwigia palustris* is cited as a perennial, but Hegi (1926) recognises that it may be either annual or perennial. Babington (1851), Withering (1833) and Townsend (1883, 1904), who probably knew it well in the New Forest, as well as Deakin (1857), all give it annual status. It probably shares with other characteristic 'mud species' the propensity to fruit most freely in proportion to size when growing on mud and then often to behave as an annual (Salisbury 1970). Plants cultivated on mud were found to be either annuals or short-lived perennials. As a partially submerged aquatic, *Ludwigia* is much larger but flowers and fruits far less freely in proportion. It may certainly then perennate in Hampshire but perhaps only when the winter is not severe. Numerous mature plants were seen in two locations in July 1969, of which most were dead or decrepit in late October, although younger plants were flourishing.

Descriptions of the fruits of *Ludwigia palustris* in most Floras are inadequate and even liable to mislead, being perhaps based upon herbarium material. Ripe capsules are slightly conical with a rounded base, frequently almost bell-shaped. They are four-sided, with rounded angles that correspond within to roughly triangular columns of parenchymatous tissue with numerous intercellular spaces largely responsible for the buoyancy of detached fruits. The capsule at maturity is pale yellow with greenish stripes marking the very thin membranous portions of the fruit wall that correspond to the four loculi and potential lines of rupture.

These bands are puckered, perhaps due to pressure from the developing seeds immediately beneath (Fig. 1).

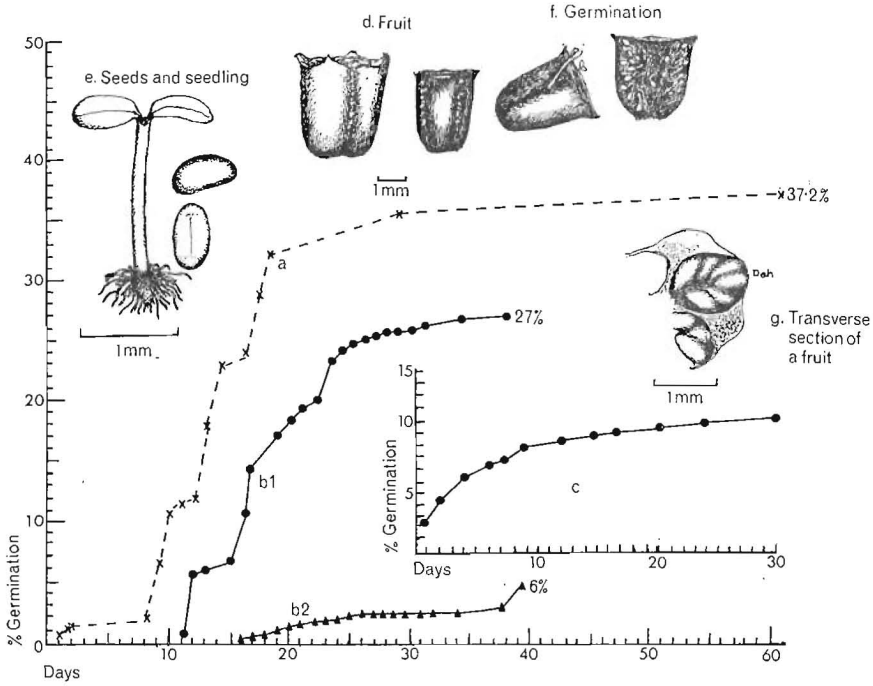

FIGURE 1. Germination of *Ludwigia palustris*. a. Germination of 593 seeds sown on the 24th August and exposed to light. b1. Germination of seeds of another plant also in light. b2. Germination of seeds from plant b maintained in darkness. c. Germination of a sample of 900 seeds at 25°C. Inset are shown: d. fruits as shed; e. seeds and seedling; f. germination within an undehisced capsule after floating in water for two and a half months and a similar capsule split in half to display numerous seedlings within; and g. part of a transverse section of a capsule indicating where dehiscence should occur (Deh).

Material from three separate stations in the New Forest, observed over several seasons, exhibited a range of fruit size from 3 × 2 mm to 6 × 3·5 mm. The fruits become detached when ripe and fall on the mud or water surface still intact. In no instance was the fruit found to have dehisced prior to being shed. Mature fruits shaken up in water continue to float, so that water currents are probably the most frequent means of local dispersal. Ultimately the membranous portions of the fruit wall may break down, and the small seeds, if thus liberated, could then be dispersed more widely by adhesion to the feet of mud-frequenting birds. Examination of a large number of specimens, including the largest and smallest found, showed a range in number of contained seeds from 45 to 226. The average was found to be 120 $\pm$ 2·7. The individual seeds have been described as cylindrical but in side view they are seen to present a somewhat bean-like appearance (Fig. 1e). The observed size range was 0·6–0·8 mm in length, by 0·3–0·4 mm in breadth. The average weight, based upon random samples numbering about 3000 seeds from several plants, was 0·000041 gm.

In the dry summer of 1970 one patch of *L. palustris* in the Brockenhurst area

was completely terrestrial. All the plants were small and deeply pigmented. The decussate leaf arrangement, so conspicuous in aquatic specimens, was here obscured largely through internodal growth, so that the leaves approximated to a leaf mosaic in one plane (Fig. 2 A). The leaves were small and exceptionally elliptical with a relatively long and slender stalk (Fig. 2 B). A random sample of capsules from these terrestrial plants revealed an average seed content of 73 (maximum 103). The much lower seed production is not surprising, since these completely terrestrial plants are much smaller than the partially submerged plants growing in shallow water and a typical leaf of the former has only about one-fifth the assimilatory surface of the latter.

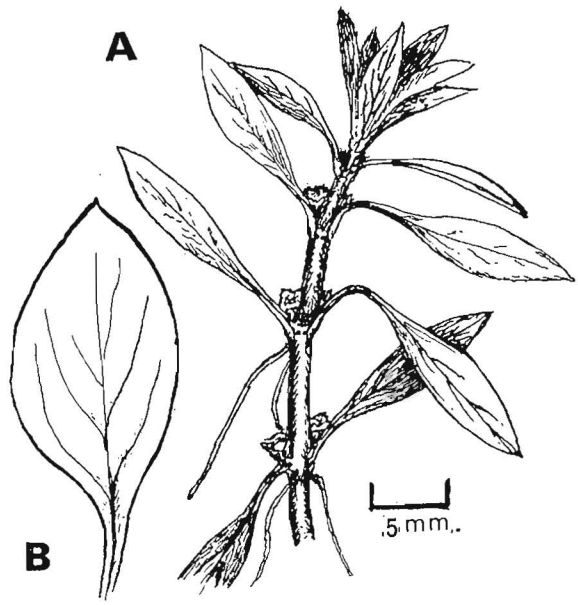

FIGURE 2. A. A terrestrial plant of *Ludwigia palustris* from Hampshire showing narrow leaves in approximately one plane. B. Leaf of aquatic plant from the same locality.

A number of germination experiments have been carried out with seeds from freshly shed fruits; but it must be appreciated that these were removed from the capsules, whereas in nature they would perhaps have remained till the fruit wall ruptured or decayed. These precociously liberated seeds exhibited a marked approach to the quasi-simultaneous type of behaviour that characterises so many 'mud species' (Salisbury 1970), although the total germination of seeds from Hampshire plants has never been high. In one sample of about 600 seeds sown in 1968 only 37·2% germinated, but 80% of these did so within the first ten days (Fig. 1 a). A very small percentage may germinate in darkness (Fig. 1 b2) but the majority do not. In one sample 6% germinated in the dark, but only after 39 days, although about 2% had germinated only a few days later than those in the light.

Freshly shed fruits, which, be it noted, had not become dry, were placed in water on October 16th, exposed to daylight and maintained in fluctuating temperatures which ranged from a minimum of 4·5°C at night to a maximum of

16·4°C in the day. Most fruits were still floating and intact after three months. In most of the capsules some of the seeds had germinated. Seedlings had emerged through the thin parts of the fruit wall (Fig. 1 f) and a fruit split open is figured to display the germinating seeds within. By January 30th the capsules, otherwise unruptured, had produced from 7 to 32 protruding seedlings (average 19·5). A few capsules had however ruptured into two or four segments, liberating seeds of which an appreciable proportion germinated and continued their growth under water, thus emphasising that desiccation is not required to stimulate germination. By the end of January there was a total of 375 seedlings representing a germination of only about 12·5%. Three other samples harvested in mid-October, of 567, 472 and 220 seeds respectively, were also maintained in warm conditions and yielded total germinations of 10·9%, 6·0% and 7·7%. Yet another sample of 594 seeds taken from floating fruits in November yielded under 4%. The contents of nine other capsules numbering over 900 seeds were sown and maintained at a higher temperature of 25°C but the germination, though initially accelerated, only attained 11·3% (Fig. 1 c).

To ascertain if a longer period of ripening was required, seeds were dissected out of undehisced capsules in March. 2114 were sown, exposed to light at between 19°C and 25°C. Germination began in eight days and continued for thirty-six, attaining a total of 16·9%. So the lapse of time and more prolonged ripening would appear to neither augment nor diminish viability.

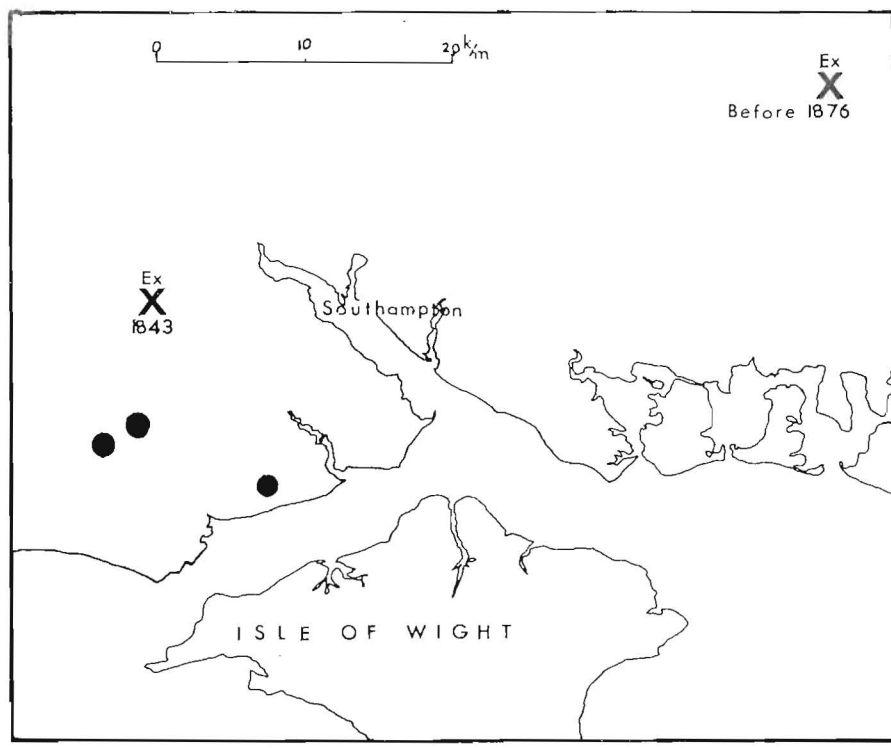

FIGURE 3. Sketch map showing the distribution in Hampshire of localities from which *L. palustris* has been recorded. Ex. probably extinct.

In Britain the capsules obviously fail to dehisce and Dr P. H. Raven states (*in litt.*) that in his experience the capsules 'never dehisce regularly anywhere in the world, and always rot apart'. This failure must greatly handicap dispersal and may in part at least account for its failure to spread in England, although the distribution of *L. palustris* would suggest that climatic conditions are unfavourable. In France, for example, it would appear to have been frequent only in the south (Grenier & Godron 1849). The sketch map (Fig. 3) shows the distribution of all the Hampshire records, which are consistent with the concept of inefficient dispersal.

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