

Mechanisms of establishment and spreading of *Cyperus rotundus* – the worst weed of warm regions

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Summary

Establishment of *Cyperus rotundus* is rapid and its spatial expansion is continuous under a wide range of moisture and temperature conditions; minimum temperature is 20°C for sprouting and growth, and 0°C for tuber viability. Rhizomes extend in the soil profile and form either tubers in chains or basal buds related to aerial shoots. Tubers bear numerous buds, the sprouting of which is regulated by apical dominance; dormant buds remain viable in soil for prolonged periods. Damage to shoots, tubers or rhizomes triggers sprouting of dormant buds and renewed growth. Propagation is primarily by tubers, and rarely by seeds.

Introduction

Cyperus rotundus L. (purple nutsedge) is considered to be the worst weed in the world, because of its ubiquitous presence in warm regions, its propagation potential and strong competitive capacity, and the difficulty to control, when established, by mechanical or chemical means. Purple nutsedge is believed to be a native of the tropics (14). This weed has spread with the development of intensive, irrigated agriculture in warm countries, and through the increased international transport of plant material (2,5). It occurs at present in more than 90 countries, on most continents, on agricultural and uncultivated land, under tropical, subtropical and Mediterranean climates, between latitudes 35° N and 35° S (6,14,21).

In this paper I examine the mechanisms of establishment, propagation and dissemination which combine to make this species such a serious pest to cultivated crops. Where data are available, the characteristics of purple nutsedge will be compared with *Cyperus*

esculentus L. (yellow nutsedge), a related perennial infesting warm and temperate zones. In the text, *C. rotundus* and *C. esculentus* are designated by CR and CE, respectively.

Establishment and development

In most cases, an infestation of nutsedge starts with a tuber. The tuber sprouts and forms roots and a rhizome which extends vertically and develops an aerial shoot with a swelling ('basal bulb') at its base. Subsequently, rhizomes are produced by buds located on tubers and on basal bulbs, and grow either into new aerial shoots with a basal bulb or expand plagiotropically and form new tubers. On CE, tubers are terminal, whereas on CR they develop on rhizomes in chains of up to fifteen tubers (5,22).

Basal bulbs and tubers function both as storage and reproductive organs. They differ mainly by their position; basal bulbs are directly connected to an aerial shoot. As rhizomes elongate they form tubers and ensure the translocation of nutrients and assimilates between above-ground and underground parts.

After planting a tuber under suitable conditions, a shoot emerges 4 – 7 days later, and 15 – 30 days later a new tuber is formed. At that stage the plant is 'established' as it is capable of spreading or surviving even following the destruction of the aerial parts (4,5,9). In young plants, shoot development is swift, followed by a rapid increase in tuber formation (5,9).

The number of tubers produced by a CR plant is considerable. In Israel, established plants formed more than 200 new tubers and basal bulbs per m² per week (8). In Georgia, U.S.A., planted tubers produced 1000 bulbs and 2300 tubers per m² by 20 weeks after planting, with a dry weight of 3 kg m⁻² (5). Differences in the rate of tuber formation are related to climatic and edaphic conditions (14). After forming a dense network, the tuber population tends to stabilize or even slightly decrease in subsequent seasons (19).

Under similar conditions fewer, smaller tubers are produced by CE than by CR, however, the seasonal tuber production of CE is also remarkable; a tuber reportedly produced 1900 shoots and 7000 tubers in one year (20).

Factors affecting sprouting and development of tubers

Apical dominance and dormancy.

Ten or more buds are located on a tuber, and their sprouting is regulated by apical dominance. On CR, apical tubers in the chain and apical buds of the tuber sprout first, inhibiting development of more distant buds. Within an intact network, quiescent buds and chain tubers retain viability while remaining dormant for prolonged periods (14,16,19,22).

Fifty to one hundred percent of CR tubers, collected all year round from plants of various ages, sprouted under adequate temperature and moisture conditions without marked seasonal differences. Newly formed tubers also sprouted readily (10). Tubers of CE showed a clear seasonal dormancy, with those overwintering having a higher sprouting capacity than those produced in autumn (15,19,20).

Severing the tubers or the connecting rhizomes, for example, by cultivation, breaks the dormancy of the chain and induces sprouting. Mechanical or chemical suppression of the top-growth is followed by prolific emergence of new shoots (10,14,16). Inhibitory compounds present in the foliage and the tubers are probably involved in dormancy (14).

A viable tuber can sprout several times before its food reserves are exhausted. The longevity of tubers in soil is apparently related to the low oxygen level in the soil profile, which induces dormancy, and therefore increases with depth. Dormant tubers of CE are reported to remain viable in soil for 3–5 years (15).

Temperature

Minimum, optimum and maximum temperatures for sprouting of CR tubers are approximately 20, 30–35 and 45°C respectively (4,10,21). Under alternate temperatures, some sprouting may already occur at a temperature above 15°C, causing early competition to crops planted in spring.

Shoot and tuber formation are closely related to temperature changes. Plant growth is slow below 20°C, and most rapid at 26–35°C

(3,5,14,21). With decreasing temperatures the shoots wither. However, the vascular system of rhizomes remains intact after the aerial parts have decayed and the tubers formed on them overwinter (22).

Tubers of both types of nutsedge maintain their viability at the maximum temperatures recorded in most warm regions; it is the minimum temperature which determines the seasonal development and the geographical distribution of the species. Tubers of CR exposed to 2°C for 3 months lost their germinability (18). In North America the expansion of CR is limited by the isotherm of –1.1°C average minimum air temperature in January, corresponding to 0°C at 10 cm soil depth (18).

Tubers of CE are more resistant to low temperatures than CR; their minimum sprouting temperature is 12°C and tubers may tolerate –20°C during winter (15,19).

Moisture

CR grows in a wide range of soil moisture, including flooded soil (17,21). Tubers sprout readily between 20% and 80%, and most rapidly at 40–60% field capacity. Tubers did not sprout in water with a low oxygen level, but maintained their viability even when steeped in water for 200 days (4,11,14,21).

Desiccating the tubers, in shade or in sunshine, reduces their sprouting capacity. As the moisture content of tubers (normally 55–70%) decreases below 10–12%, germinability is lost (12). A system of CR control has been developed in areas with a hot and dry summer, based on deep tillage which cuts the tuber chains from their moisture supply and causes their desiccation (1).

Light

Tubers sprout normally in the dark and are also able to sprout in white and coloured light (21). Both CR and CE possess the C₄ dicarboxylic acid photosynthetic pathway, which allows plants to assimilate CO₂ efficiently at high temperatures and light intensities (19,22).

The shoot and tuber production of both nutsedges is correlated with the intensity of photosynthetically active radiation, and is sensitive to shading (19). Decreasing the incident light intensity by shading with plastic sheets, or with companion plants, causes etiolation of the shoots and reduces tuber formation (5,14). However, only a completely

opaque cover, laid on the soil for a prolonged period, can eradicate a severe infestation of purple nutsedge.

In CE, short photoperiods stimulate tuber formation and long photoperiods promote shoot development (5,15,19). In CR the effect of photoperiod is less pronounced, particularly in regions with limited fluctuations in daylength (10,14).

Depth

In established plants of CR, the subterranean system, rhizomes and tubers, is generally concentrated in the upper 15 – 20 cm of soil. Tubers have been recorded deeper, but rarely lower than 50 cm (10,19,22). Rhizomes penetrate and form tubers deeper in light-textured or frequently cultivated soils than in heavy soil (1,3,10,21).

The depth at which tubers sprout in soil is limited by the available oxygen necessary for germination, and the amount of food reserves in the tuber required to form a rhizome sufficiently long enough to reach the soil surface – where it will produce a basal tuber and emerge as a shoot. Under experimental conditions, tubers of nutsedge sprouted and formed aerial shoots from a depth of 45 cm (9,17,19) and occasionally even deeper (4). Sprouting percentage and rapidity of emergence decrease with increasing depth, although at the end of a growing season the total number of tubers produced is similar for both early- and late-emerging plants (9).

Time and depth-regulation of tuber sprouting have many important implications. As practically all underground tubers are capable of forming new plants, herbicidal treatments are only effective if the active compound is translocated to all tubers. Also solarization, which produces lethal temperatures of 50 – 60°C close to the soil surface, is insufficient to eradicate an established stand of nutsedge. On the other hand, burying tubers deep in the soil, by ploughing for instance, will not reduce the infestation.

Expansion and dissemination

Spatial expansion

Spreading of CR from a single tuber was followed during two seasons in Israel (10). Three months after planting, shoots emerged up to 110 cm from the original tuber. The expansion proceeded radially, at first following the path of the rhizomes. After six months

a continuous infestation had been formed covering 7.6 m², and up to 2.8 m from the loci. At the end of the second season, the infestation was 56 m² and extended up to 5.4 m from the loci. Spread was slower during the cool season, as all shoots wilted, and accelerated again in spring.

The mean increase in area for the study period was 2.8 m² per month, compared to 0.6 m² and 0.9 m² per month for *Sorghum halepense* and *Cynodon dactylon* grown under similar conditions. The rapid expansion of CR reflects the vigour of its underground system. The two perennial grasses spread by rhizomes which also function as storage and reproductive organs. In nutsedge these functions are carried out separately by compact tubers and slender rhizomes.

The rapid expansion of CR has been recorded elsewhere. For instance in Georgia, U.S.A., plants from tubers planted 90 cm apart overlapped in five weeks; after 20 weeks approximately 5700 km of rhizomes had been produced per hectare (5). CE is also characterized by rapid spread; a single tuber produced a patch 2 m in diameter after one year (20).

Dissemination by tubers

Tubers of both nutsedges are the primary dispersal unit. They sprout under appropriate conditions or remain dormant for extended periods, thus functioning like seeds of annuals (19). Tubers are spread from infested sites by, for example, people, animals, farm equipment, plant material, soil and water (2).

In urban areas transport of contaminated soil and propagation material to gardens is a major cause of spread. Tubers of edible varieties of CE are sometimes imported intentionally, and escape. In the Netherlands, tubers of CE have been introduced accidentally from warm countries with plant material, and are seriously infesting regions which produce flower bulbs such as gladioli.

Propagation by seeds

Plants of CR produce up to several thousand achenes (seeds) on each inflorescence (13,19), but their viability is low (1,3,12) or nil (6,10,14,19). In comparative studies, seeds of CE and other *Cyperus* species produced higher germination rates than CR (12).

Freshly harvested seeds of CR are dormant, presumably because of their hard seed coat, and a long period of after-ripening is required before they germinate (1,17). The half-life of

CE seeds buried 5 cm in soil was found to be about 500 days (13). Seedlings of CR have rarely been observed. In California, seedlings of CE grown in a glasshouse appeared less vigorous than sprouts of tubers, and no seedlings have been found in the field (7). In Zimbabwe, 0.8% and 0.03% of CE seeds produced seedlings under irrigated and rain-fed conditions, showing that adequate soil moisture is critical for establishment (13).

Genetic analysis of populations of both nutsedge species found in California exhibited limited genetic variability, indicating primarily asexual reproduction, even for CE (7). Most authors (6,14,15) conclude that for each of these species, propagation by seed is not the most important means of spread, even though viable seeds constitute a source of infestation (1,12,13).

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