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Common evening-primrose (*Oenothera biennis* L.)

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Primroses, The spring may love them; Summer knows but little of them.
Foresight. William Wordsworth, 1819

Ring-ting! I wish I were a Primrose
A bright yellow Primrose, blowing in the Spring!
Wishing. William Allingham

"The snowdrop and primrose our woodlands adorn, and violets bathe in the wet o' the morn."
Robert Burns

Introduction

Common evening-primrose (*Oenothera biennis* L.) is a member of the Onagraceae, which is often referred to as the willow herb or evening-primrose plant family. Modern classification schemes include the Onagraceae in the order Myrtales, with such families as the Myrtaceae, Melastomataceae, and Lythraceae, because they share some characteristics, such as a distinctive hypanthium (i.e., floral cup) and internal phloem (i.e., located to the inside of the primary xylem) (Dahlgren and Thorne 1984). The members of this family are characterized as annual, biennial, or perennial herbs or sometimes shrubs or trees; members are terrestrial or, rarely, aquatic plants (Dahlgren and Thorne 1984; Zomlefer 1994). The Onagraceae consists of 22 genera and approximately 650 species that are found in temperate and subtropical regions, with the greatest amount of species diversity occurring in the New World, particularly the western United States and Mexico (Wagner and Hoch 2019). Common evening-primrose, itself, is native to North America (Frankton and Mulligan 1970). *Oenothera* is one of the major genera in the Onagraceae and consists of 145 species (Wagner 2017), many of which are referred to as evening-primroses. Several members of the *Oenothera* are considered ornamental plants, along with other genera in the primrose family, including *Clarkia* (farewell-to-spring, godetia), *Fuchsia* (lady's ear drops), and *Gaura* (Zomlefer 1994).

Etymology

Carl Linnaeus, in his *Systema Naturae*, provided the modern genus name *Oenothera*, which is derived from the Greek words *oinos* ("wine") and *thera*, which has several meanings (depending on the interpreter), including "scenting" and "to imbibe" (Wagner 2017). One story suggests that when the root was eaten, it allowed a person to drink a greater quantity of wine (Horn and Cathcart 2005). The specific epithet, *biennis*, refers to the plant's life cycle, which is biennial. The full common name recognized by the Weed Science Society of America is "common evening-primrose" (WSSA 2019). The descriptive name, "evening-primrose," describes the tendency of the plants to completely or partially close their flowers during the day (Britton and Brown 1898). The plant's other common names include candlestick, coffee-plant, common eveningprimrose, evening primrose, hoary evening primrose, cureall, cure-all, king's cure-all, fever-plant, four-o'clock, German rampion, golden candlestick, hog weed, large-rampion, night primrose, night willow-herb, scabious, scabish, scavey, scurvish, speckled-John, sundrops, tree primrose, Victoria's evening primrose, weedy evening primrose, yellow evening primrose, and onagri bisannuelle (Bailey 1963; Bergen 1893; Bryson and DeFelice 2010; Coffey 1993; Horn and Cathcart 2005; Miller and Miller 1999; Muencher 1955; Stubbendieck et al. 1994). Common evening-primrose and other *Oenothera* spp. are not closely related to the true primroses, which are in the genus *Primula*.

Description

O. biennis has been described in varying detail by Gleason and Cronquist (1991), Zomlefer (1994), Miller and Miller (1999), Bryson and DeFelice (2010), and Wagner (2017); the following summary is derived from these sources. Common evening-primrose is an erect biennial that can grow to heights of 2 m. A deep, fleshy, fibrous taproot anchors the plant in the ground.

Seeds germinate in the summer or fall and give rise to rosette leaves that are 5- to 30-cm long and 1- to 7-cm wide. Rosette leaves are alternate, with long petioles and blades that are lanceolate, pubescent, and have tips that are gradually pointed. Leaf margins are entire to sometimes shallowly dentate or wavy. Cauline leaves are up to 15-cm long and 4-cm wide, alternate, lanceolate, pinnately veined, and are sessile or else held on short petioles. Stems produced the second year are erect, stout, and branched with short, appressed trichomes often giving them a reddish appearance. Plant tissues contain raphides (i.e., bundles of needle-like calcium oxalate crystals) and tannins.

Oenothera flowers occur in a terminal spike that can be 0.6 m or more long. Mature buds are erect and curve upward. Flowers are regular, perfect, and sessile in the leaf axils. The corolla has four obovate petals that are yellow fading to pale reddish and 1.0- to 2.5-cm long. Floral tubes are 2- to 5-cm long, slender greenish-yellow, pubescent, with glandular or plain trichomes. Stamens as long or longer than the stigma and style. There are four greenish-yellow sepals that are reflexed at anthesis. An interesting attribute of the Onagraceae is their distinctive pollen characteristics. Pollen grains may occur in tetrads or monads, are relatively large, and are more or less triangular due to three protruding, stopper-like apertures. Pollen grains are connected with viscin threads, which are composed of an elastic and somewhat viscid material. Viscin threads may vary in number and structure. These slender strands also occur on pollen of certain Ericaceae.

Darlington and Steinbauer (1961), Gleason and Cronquist (1991), Zomlefer (1994), Miller and Miller (1999), and Bryson and DeFelice (2010) have all described the fruiting structures and senescence of common evening-primrose in some detail. Fruits are a capsule that is 1.4- to 3.5-cm long and 3.5- to 6-mm thick near the base, strigose to subglabrous, four-celled, four-angled, and many-seeded. Capsules gradually split from the tip downward to the base, progressively releasing the seeds. Seeds occur in two rows in each locule. Seeds are 1.3- to 1.6-mm long, sharply angled, irregularly shaped, pyramidal with a varying number of sides, reddish-brown, ridged, and often have winged edges. Because they have no special adaptations for dispersal, most seeds are released close to the parent plant. Seeds may remain viable in the soil for decades (Darlington and Steinbauer 1961). Although the parent plants die after setting seeds, the erect and leafless stems often persist into winter (Bryson and DeFelice 2010; Miller and Miller 1999; Gleason and Cronquist 1991; Zomlefer 1994).

In the southern United States, common evening-primrose plants will typically flower from June to October. The attractive and scented yellow flowers typically open at dusk (hence the name "evening primrose") in synchrony with the nocturnal feeding habits of primary pollinators (especially Hymenoptera and Lepidoptera) (Horn and Cathcart 2005; Mabberley 1997; Zomlefer 1994). Flowers remain open until morning and potentially longer on cloudy days. Nectar is secreted at the base of the style or by nectaries within the lower part of the hypanthium and accumulates in the floral tube. The pollen sticks to insects by means of the viscin strands that form between the pollen grains. Cross-pollination is generally promoted by protandry, although self-pollination is prevalent in this family as well (Zomlefer 1994). Reproduction is by seeds, which may be dispersed by wind and birds.

History and Distribution

Pollen from the Onagraceae "appears in generalized form in the Maastrichtian, and in gradually increasing diversity form the Eocene onwards" (Gleason and Cronquist 1991). The genus *Oenothera* may have spread from Central to North America between the successive ice ages of the Pleistocene epoch. The prolific genetic diveristy of this genus may be due, in part, to hybridization between survivors of different colonizing events. Common evening-primrose is now endemic to much of North America, ranging from Mexico to Florida; north to central Ontario and Quebec, Canada; and west to North Dakota and Oklahoma. It can also be found along the Pacific coastline of North America (WSSA 2019).

From its origins in North America, *O. biennis* has been moved by man and become established in all other continents, excluding Antarctica. Its first documented introduction to Europe was in 1870 in England; it was imported for its medicinal qualities. From there it became well established through much of Western Europe. During the 1960s, there was a measurable increase in the area invaded by common evening-primrose, which was characterized by spread into central and eastern Europe. Interestingly, the proliferation of *Oenothera* spp. in Europe has actually occurred because of the influx of two distinct groups of this genus. The biennial species of common evening-primrose, which originated from North America, is reported to be well adapted to inland conditions in Europe (which has lower mean temperatures and more balanced monthly precipitation) as compared with annual and perennial *Oenothera* spp. originating from South America, which favor a more oceanic climate. Common evening-primrose has also spread to Japan, Australia, and South Africa, and has become established, or is becoming established, in most other temperate environments around the globe (Frean et al. 1997; Holm et al. 1991; Mihulka and Pysek 2001; Miller and Miller 1999; Stadler et al. 1998).

The literature on the Onagraceae, especially the genus *Oenothera* (e.g., Cleland 1972), is extensive, with many studies focused on embryology, cytology, chemistry, and evolutionary ecology; *O. biennis* was one of the earliest model species in genetics and cytogenetics. (Conti et al. 1993; Johnson 2011). According to Johnson (2011) *O. glaziovana* Micheli, in Martius, which is a hybrid of *O. biennis* and *O. elata* subsp. *Hoookeri*, played a role in the rediscovery of Mendel's laws of inheritance through the independent assortment of alleles. This is despite that many *Oenothera* (at least 43 species), including common evening-primrose, do not display independent assortment, owing to permanent translocation heterozygosity. With permanent translocation heterozygosity, progeny are genetically identical to their parent plant, because of a lack of recombination and segregation.

Characteristics

Toxicity

There are no known toxicity issues related to *O. biennis* (Bryson and DeFelice 2010).

Weediness

Common evening-primrose has moved around the globe, primarily by the actions of man, in part because of its value as a popular flower. *O. biennis* was included in one of the first recorded collections of American native plants. John Bartram (1699–1777), a Quaker gardener and botanist, established his famous garden near Philadelphia, PA, which included 12 different types of evening-primroses (Horn and Cathcart 2005). Unfortunately, the plant is a great opportunist and has become a regular inhabitant of disturbed habitats in multiple countries, including the

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United States, Canada, Japan, and South Africa (Holm et al. 1991; Miller and Miller 1999). The species' preference is for full sun, average moisture, and a soil that is somewhat sandy, although other growing conditions are adequate. It tends to favor disturbed areas in both natural and developed habitats, including soil and sand prairies, abandoned fields, thickets, glades, roadsides and railroads, slopes of drainage ditches, vacant lots, and so forth (Hilty 2018). It is an early invader of new forest plantations (Miller and Miller 1999).

Common evening-primrose seeds exhibit an annual nondormancy; that is, a conditional dormancy cycle, being nondormant from midwinter to late spring and conditionally dormant in summer and autumn (Baskin and Baskin 1994). Light is not a requirement for the germination of buried *O. biennis* seeds (Baskin and Baskin 1994), because the seeds can germinate in darkness in spring and summer at simulated habitat temperatures. Common evening-primrose's long-lived seed has likely contributed to its weediness. Seeds of *O. biennis* were part of Beal's famous seed-longevity experiment initiated in the fall of 1879 (Beal 1905). In this study, Beal selected seeds from 23 common plants, combined 50 seeds of each species with moist sand, and put the mixtures in unsealed pint bottles. He then buried the bottles in a sandy knoll on the Michigan State University campus. The protocol was to unearth the seeds periodically to determine the length of time the seeds would remain dormant in the soil but still germinate under favorable conditions. After 80 years, only three species exhibited viable seed: curly dock (*Rumex crispus* L.), moth mullein (*Verbascum blattaria* L.), and common evening-primose (Darlington and Steinbauer 1961). Moth mullein had a 70% germination rate at this assessment timing, followed by common evening-primrose (10%) and curly dock (2%). No seeds of common evening-primrose germinated after being buried for 90 years (Kivilaan and Bandursky 1973).

Common evening-primrose has been documented to be only marginally sensitive to glyphosate and dicamba (Olszyk 2015), which are used for weed control in many different crop and noncrop systems.

Uses

Many indigenous peoples in North America used *Oenothera* spp. generally (and common evening-primrose, in particular) for food and medicinal purposes (Borchers et al. 2000; Moerman 1998). For example, the Cherokee cooked and ate common evening-primrose leaves as greens and boiled the roots like potatoes (Hamel and Chiltoskey 1975; Perry 1975). Seeds had several uses. Members of the Gosiute used them for food, and the Lakota are reported to have burned them as incense. The Potawatomi used the tiny seeds as a medicine for unspecified ailments (Chamberlin 1911; Rogers 1980; Smith 1932a). The Ojibwa tribe soaked the whole plant and applied it to bruises (Smith 1932b). The Iroquois, Cherokee, Ojibwa, and Potawatomi peoples used *O. biennis* to varying degrees as a dermatological aid, a hemorrhoid remedy, a treatment for premenstrual and menstrual pains, and a stimulant and strengthener (Borchers et al. 2000; Hamel and Chiltoskey 1975; Herrick 1977).

Culpeper's *Complete Herbal* stated the primroses were a commonly used remedy and the leaves could be made into a salve to heal wounds (Culpeper 1653). Common evening-primrose extracts inhibit *Escherichia coli* and *Staphylococcus* spp. (Hayes 1947). Seeds are a source of γ-linoleic acid, important in production of fatty acids and prostaglandins and used in the treatment of premenstrual tension (Mabberley 1997). The seed oil has been investigated experimentally for treating a wide variety of conditions, including eczema, asthma, inflammation, premenstrual syndrome, breast problems, metabolic disorders, arthritis, and alcoholism (Coffee 1993). Common evening-primrose is a source of a pain-relieving compound used for headaches and a remedy for venereal disease and eruptions of the skin (Horn and Cathcart 2005). Complementing the aforementioned indigenous knowledge, there is documentation that, during the first year of growth, the young roots may be boiled and eaten as a vegetable and the shoots, fruits, and seeds may be consumed (Coffee 1993; Horn and Cathcart 2005; Mabberley 1997).

Common evening-primrose has nutritional value for wildlife, such as various small mammals, as well as white-tailed deer. Birds, including the northern bobwhite, mourning dove, American goldfinch, and dark-eyed junco, consume the seed (Kindscher 1987, Mabberly 1997; Miller and Miller 1999; Stubbendieck et al. 1994). The flowers are nectar sources for many moths and butterflies, particularly sphinx moths (Hilty 2018; Miller and Miller 1999). Several species of bees, including honeybees and bumble bees, have been reported to visit common evening-primrose flowers seeking nectar and/or pollen (Hilty 2018). In addition, the larvae of some moths and beetles consume *O. biennis* plant parts. Numerous species of aphids and adult beetles feed on the foliage, including adult Japanese beetles (*Popillia japonica* Newman) (Hilty 2018).

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