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OBSERVATIONS OF HERMAPHRODITIC LATE-SEASON FLOWERING IN THE RED OAK *QUERCUS AGRIFOLIA*

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ABSTRACT

For three consecutive years (2015–2017) a single coast live oak (*Q. agrifolia* Née) in the city of Santa Cruz, California, has produced bisexual (perfect) flowers on crown twigs emerging mid to late summer. By the end of each year many of these flowers developed into small acorns, though none of the fruit ever matured completely or survived until the following year.

True oaks (*Quercus*) are normally monoecious. Nevertheless, hermaphroditic flowers have been documented in white oaks (sect. *Quercus*) by a number of researchers, but only once in red oaks (sect. *Lobatae*).

The earliest described California white oak with perfect flowers was '*Quercus dumosa* Nutt.' (Greene 1889; now *Q. pacifica* Nixon & C.H. Mull.). John Tucker subsequently provided detailed reports of hermaphroditic flowers in other California white oaks — '*Q. turbinella* subsp. *californica*' (now *Q. john-tuckeri* Nixon & C.H. Mull.), *Q. durata* Jeps., and *Q. dumosa* (Tucker 1972), and also the white oak *Q. gambelii* Nutt. in Utah (Tucker et al. 1980). Papper (pers. comm., 2015) has more recently observed late-season bisexual flowers in *Q. durata*.

Other authors have documented bisexual flowers in white oaks elsewhere in the world: *Quercus coccifera* L., an oak with biennial fruit from the Mediterranean (Scaramuzzi 1958), green oak—a likely *Q. cerris* L. × *Q. suber* L. hybrid—from Croatia (Borzan & Želimir 2000), *Q. ilex* L. (Borzan & Stabentheimer 2002), and *Q. glaucoides* M. Martens & Galeotti and *Q. rugosa* Née from Mexico (Romero et al. 2000, 2007).

However, the only previously described instance of a red oak producing hermaphroditic flowers was a single coast live oak (*Quercus agrifolia* Née) on Santa Cruz Island, a California Channel Island south of Santa Barbara and west of Ventura (Greene 1889, p. 8):

> "I observed, in 1885, a well grown tree of this species, in which all the flowers were borne on rigidly erect, stout, spike-like peduncles, each flower seeming to have been perfect, and the usual pendulous staminate aments entirely absent; so that the young acorns were all spicate."

Observations

A volunteer tree of *Quercus agrifolia* in my Santa Cruz back yard bloomed copiously early in 2015, as it has done every spring, but I was surprised to notice it flowering for a second time late in the summer of that year. Beginning with that initial observation in 2015 the tree has produced late-season hermaphroditic flowers for three consecutive years. No damage to the tree was noted during that time; the amount of rainfall was markedly inconsistent from year to year.

The spring flowering of this tree was typical of what I have observed in California red oaks (Figure 1).

- Male and female flowers are always located on reproductive shoots, male catkins emerging first at the bottom of the shoot, either clustered together near the bud scar or less commonly distributed in the axils of the most proximal leaves. Female flowers if present appear later and more distally in leaf axils of the same shoot.
- Reproductive shoots may have male flowers only but never female flowers only.

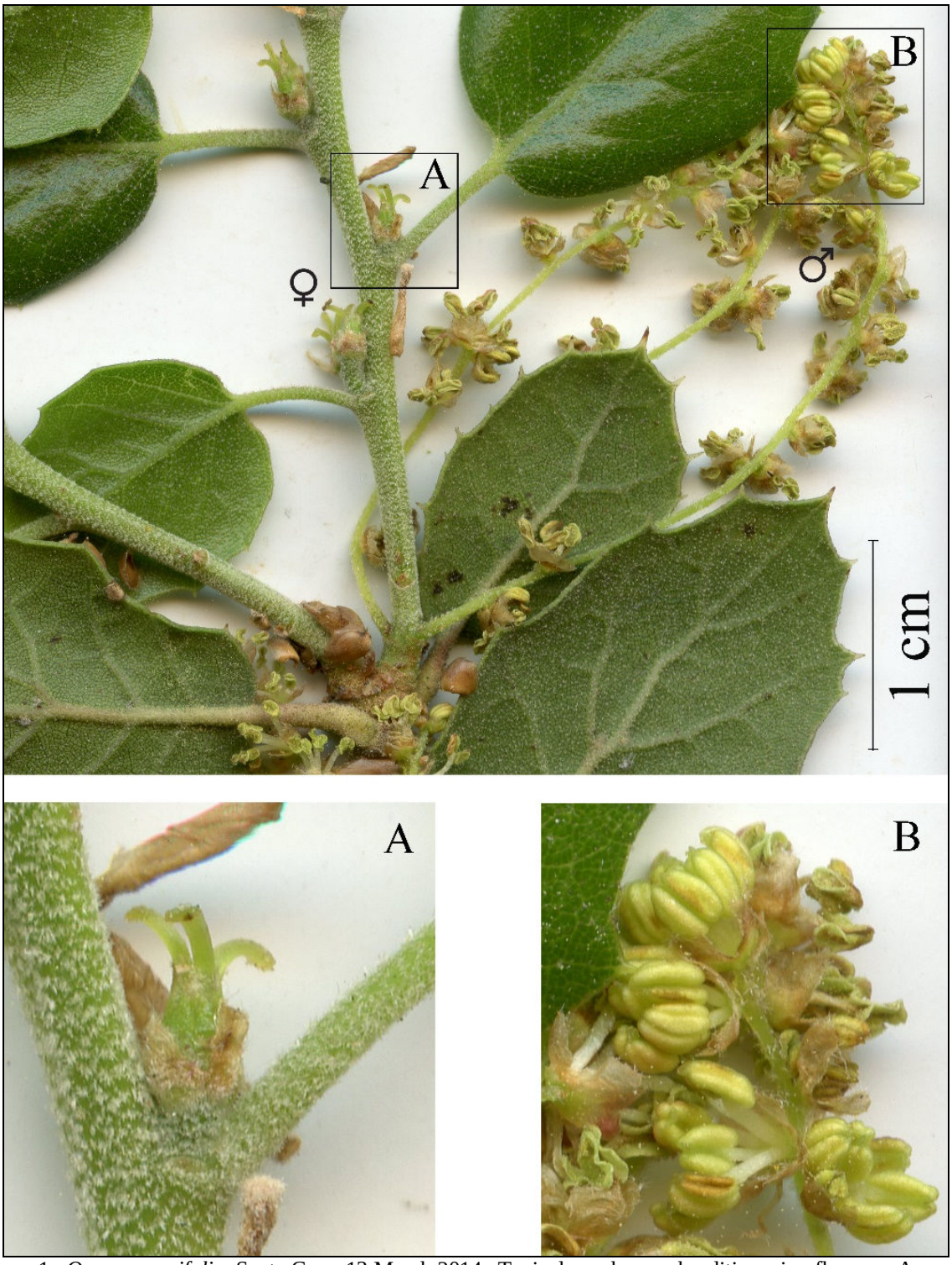

Figure 1. *Quercus agrifolia*, Santa Cruz, 13 March 2014. Typical non-hermaphroditic spring flowers. A. Female flowers, in the leaf axils of the reproductive shoot, generally in pairs. B. Male flowers, on catkins sprouting from the base of the reproductive shoot just above the bud scar.

The late-season flowering I observed, however, was quite different from the spring flowering. Reproductive shoots bore numerous female-only flowers, while structures suggestive of depauperate male catkins were only occasionally present.

By mid-August 2015 three different types of fruit were simultaneously present on the tree in my back yard: type **1**—nearly mature acorns from spring flowers; type **2**—small immature acorns with the nut barely protruding from the cupule from late season flowers; and type **3**—even smaller fruit with the nut fully enclosed by the cupule, also from late season flowers. Whereas fruit types 1 and 2 were arranged 1 or 2 per leaf axil on stout peduncles as is typical for *Quercus agrifolia*, type 3 fruit were often more numerous—sometimes 10 or more—and occasionally clustered on slender peduncles similar to those bearing spring male flowers (Figure 2).

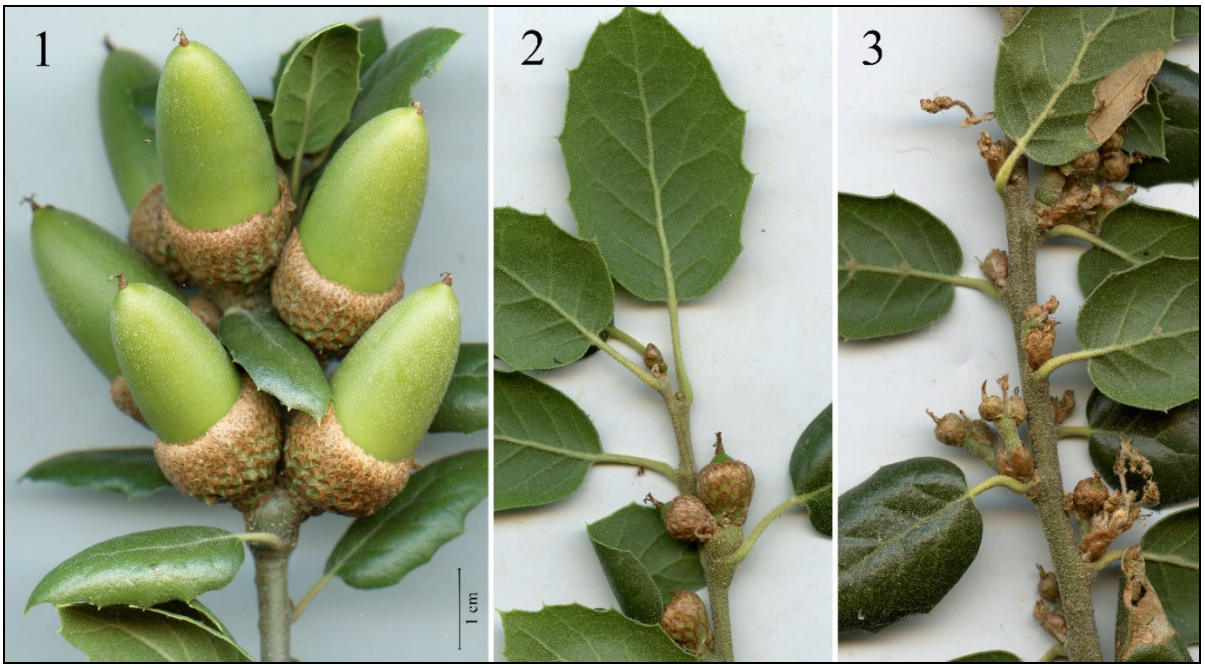

Figure 2. *Quercus agrifolia*, Santa Cruz, 14 August 2015. 1. Large fruit from spring flowers, nearly mature, fully-emerged nuts. 2. Small fruit from late summer flowers, immature, newly-emerging nuts. 3. Smallest fruit with non-emerging nuts, from late summer flowers, often numerous, sometimes on slender peduncles, occasionally mixed with type 2 fruit.

It was only later upon closer examination of the smallest fruit (type 3) in early September 2015 that unexpectedly I discovered many of them to be bisexual (Figure 3).

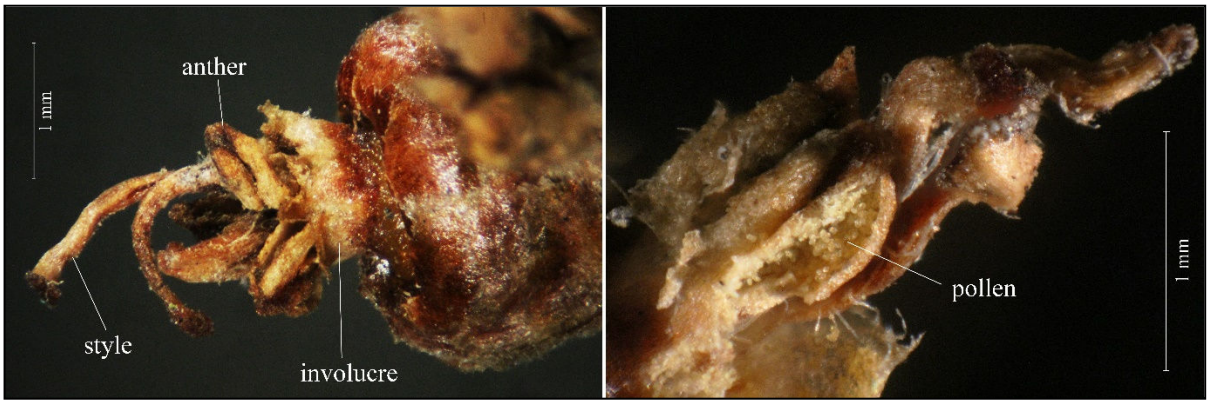

Figure 3. *Quercus agrifolia*, Santa Cruz, 05 September 2015, bisexual flowers.

The following year, after the usual heavy spring bloom and during the subsequent maturation of a large crop of acorns, fast growing twigs appeared in the tree's crown at midyear. By the end of July 2016, the new growth bore clusters of both female and bisexual flowers for a second consecutive year of late summer flowering (Figure 4).

Figure 4. *Quercus agrifolia*, Santa Cruz, 28 July 2016, newly bloomed female and bisexual flowers. Bottom A is detail from photo above.

Figure 5. *Quercus agrifolia*, Santa Cruz, CA, 28 August 2017, third consecutive crop of late season bisexual flowers.

In 2017 spring bloom and acorn maturation took place as in previous years. Mid-year twig growth in the tree's crown and subsequent late summer flowering occurred again. For a third consecutive year the tree in my back yard bore a crop of late season flowers, some hermaphroditic (Figure 5). As in prior years, none successfully matured.

Causes of hermaphroditic flowering

It is unclear what instigates the formation of bisexual flowers in oaks. Tucker (1980) suggested hermaphroditic flowering in *Quercus* might be caused by unusual environmental cues activating normally suppressed ancestral gene combinations. Atypical temperature, precipitation, or light could be factors.

Kevin Nixon (pers. comm., 2015) has speculated that damage to individual trees may cause hermaphroditism by triggering premature maturation of buds, resulting in only partially differentiated flowers. Although reproductive buds are normally formed during the previous year (Conrad 1990; Turkel et al. 1955), buds producing late-season flowers appear to form during the spring of the same year (Tucker 1980).

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