Additional morphological measurements of *Arceuthobium littorum* and *A. occidentale* (Viscaceae)

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ABSTRACT

Coastal dwarf mistletoe (*Arceuthobium littorum*) was separated from gray pine dwarf mistletoe (*A. occidentale*) on the basis of several morphological and physiological characteristics in 1992. However, when *A. littorum* was described, several key morphological characters had not been adequately quantified and recent molecular evidence has suggested it is closely related to several other dwarf mistletoes in California, including *A. occidentale*. Therefore, we made additional morphological measurements for *A. littorum* from eight populations along the coast of California and for *A. occidentale* from 28 populations distributed throughout its geographic range. We also made additional observations of the phenology of both taxa. Our data demonstrated that *A. littorum* was morphologically and physiologically distinct from *A. occidentale* using several characteristics of male plants: *A. littorum* had significantly larger staminate spikes, flower diameters, petal lengths and widths, and anther diameters. In contrast to *A. occidentale*, *A. littorum* produced fewer 3-merous staminate flowers, and it commonly produced 5-merous and rarely, 6-merous flowers. *Arceuthobium littorum* also consistently flowers and disperses seed approximately one month earlier than *A. occidentale*. Therefore, our data supported the classification of *A. littorum* as a distinct species from *A. occidentale*.
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KEY WORDS: *Arceuthobium littorum*, *Arceuthobium occidentale*, Coastal dwarf mistletoe, Gray pine dwarf mistletoe, morphology, *Pinus muricata, Pinus radiata, Pinus sabiniana*.

Arceuthobium littorum Hawksw. Wiens & Nickrent (coastal dwarf mistletoe, Viscaceae) and *A. occidentale* Engelm. (gray pine dwarf mistletoe) are parasites of pines (*Pinus* spp., Pinaceae) and are endemic to California (Hickman 1993; Hawksworth and Wiens 1996). *Arceuthobium littorum* is primarily a parasite of *Pinus muricata* D. Don (bishop pine) and *P. radiata* D. Don (Monterey pine) and is distributed along the Pacific Coast from near Fort Bragg (Mendocino County) south to Cambria (San Luis Obispo County). *Arceuthobium occidentale* is primarily a parasite of *P. sabiniana* Dougl. ex D. Don (gray pine) and is distributed in the foothills surrounding the Central Valley. These dwarf mistletoes are not sympatric, but they occur within approximately 50 km of each other in San Luis Obispo and Monterey Counties.

Prior to 1992, *A. littorum and A. occidentale* were considered to be conspecific (Peirce 1905, Gill 1935, Hawksworth and Wiens 1972, 1984) until Hawksworth et al. (1992) separated *A. littourm* from *A. occidentale* based on differences in plant and fruit size, host affinities, and the presence or absence of witches' brooms on infected principal hosts (see Table 3 in Hawksworth et al. 1992). Verticillate branching has also been shown to occur more commonly for *A. littorum* than *A. occidentale* (Mark and Hawksworth 1981). Using isozyme electrophoresis, Nickrent and Butler (1990) demonstrated that populations of *A. littorum* shared a high degree of allelic identity and were genetically distinct from populations of *A. occidentale*. However, more recent molecular work using ribosomal and chloroplast DNA failed to resolve *A. littorum* and *A. occidentale* to the species level (Nickrent et al. 2004), suggesting that further study of their morphological and physiological characteristics was needed. Therefore, we initiated this study to provide more morphological and phenological data for both *A. littorum* and *A. occidentale* so that their similarities and differences could be evaluated based on additional information.

MATERIALS AND METHODS

We sampled eight populations of *A. littorum* along the Pacific Coast based on collections reported in Hawksworth and Wiens (1996) and 28 populations of *A. occidentale* throughout its reported distribution in California (Fig. 1). For each population, 10-20 male and 10-20 female infections were collected and the dominant shoot from each infection was used for morphological measurements. Measurements were made for *A. littorum* from 5 locations where it parasitized *Pinus muricata* and from 3 locations where it parasitized *P. radiata* (Fig. 1). All of the morphological measurements made for *A. occidentale* were from locations where it parasitized its principal host, *P. sabiniana*. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification of *Arceuthobium*. The following morphological characters were measured: 1) height, basal diameter, third internode length and width, and color of male and female plants; 2) mature fruit length, width, and color; 3) seed length, width and color; 4) length and width of staminate spikes; 5) staminate flower diameter for 3- and 4-merous flowers (and 5-merous for *A. littorum*); 6) length and width of staminate flower petals; and 7) anther diameter and anther distance from the petal tip. Plants were measured within 24 hr. after collection using a digital caliper and a 7X hand lens equipped with a micrometer. Staminate spike and flower measurements were made during the peak of anthesis, and fruit and seed measurements were made during the peak of seed dispersal. Voucher specimens representing all of the populations illustrated in Fig. 1 have been deposited at the University of Arizona Herbarium (UA).

Because the times of flowering and seed dispersal for *A. littorum* were poorly known (Hawksworth and Wiens 1996), additional observations of its phenology were made during the summer and fall of 2010-2012. Additional observations of the phenology of *A. occidentale* were made during the summer and fall of 2007-2012.

RESULTS AND DISCUSSION

Although Hawksworth et al. (1992) reported that the mean plant heights for *Arceuthobium littorum* and *A. occidentale* were distinctly different (12 and 8 cm, respectively), we found the mean heights of the plants were nearly identical when comparing male and female plants together (10.4 cm). Mean plant heights also varied between the male and female plants, but the differences were not statistically significant (Table 1). The most conspicuous difference between the plants of *A. littorum* and *A. occidentale* was their shoot color. While color is often an unreliable and/or less informative character for distinguishing dwarf mistletoes, the shoot color of these species was markedly different. Plants of *A. littorum* were consistently dark green, brown-green, or sometimes yellow-brown, while those of *A. occidentale* were glaucous and yellow, yellow-green, or straw. Plants of *A. littorum* were rarely glaucous and when it was observed it was a very thin waxy coating and present only near the base of plants. In contrast, plants of *A. occidentale* were frequently glaucous over their entire length, as reported by Hawksworth and Wiens (1996).

The mean basal diameter of plants was larger for *A. littorum* (3.5 mm) than for *A. occidentale* (3.1 mm), but not as great as the difference for this character reported by Hawksworth et al. (1992) (3.4 versus 2.3 mm). While Hawksworth et al. (1992) only reported a maximum basal diameter of 4 mm for

A. occidentale, we measured plants of both sexes that had basal diameters ≥ 6 mm which resulted in a larger mean basal diameter for the populations we sampled. Nevertheless, the mean basal diameter of the plants we measured for *A. littorum* (both sexes combined) was significantly different from the mean basal diameter for *A. occidentale*. In Table 1, we present the mean basal diameter of plants by sex and these values were also significantly different.

Because Hawksworth et al. (1992) reported the length and width of the third internode for the plants they measured, we also measured these dimensions. Our measurements indicated that the mean length and width of the third internode of *A. littorum* were significantly larger than those of *A. occidentale* for plants of both sexes (Table 1). The use of third internode dimensions as a taxonomic character, however, is not accepted by all investigators who have studied dwarf mistletoes. Kuijt (1970) demonstrated that dwarf mistletoes have basal meristems, and therefore, internodes may elongate for many years. This led Kuijt (1970) to discount the use of third internode dimensions, and we agree that the length of third internodes should not be used as a key character to separate taxa of *Arceuthobium*. However, we have continued to use the dimensions of the third internode for comparing dwarf mistletoes because the width of the third internode provides a relative measure of the robustness of plants beyond that of only using their basal diameter. Combining measurements of basal diameter and the width of the third internode provides a quantitative method of comparing the overall shoot thickness of the plants between species. Because Hawksworth and Wiens (1972, 1996) have long used the third internode for their studies of dwarf mistletoe morphology, we have followed this convention.

Although the length and width of staminate spikes is extremely variable for most species of dwarf mistletoes, staminate spike morphology can be taxonomically informative when it is quite distinct from other species. For example, staminate spikes of *Arceuthobium strictum* Hawksw. & Wiens are distinctive in that they often don't branch and may be as long as 6-13 cm (Hawksworth and Wiens 1996). We noted a similar characteristic for *A. littorum,* in that staminate spikes were often un-branched and were sometimes nearly 6 cm long. Moreover, some male plants emerging from an infected branch did not branch and were almost 5 cm in height. We did not observe this pattern of staminate spike production for *A. occidentale*, but some staminate spikes of this species that diverged off of the main shoot were unbranched and reached lengths of over 3 cm. However, this growth pattern for staminate spikes of *A. occidentale* was rare and most of its staminate spikes were about 1-2 cm long. The mean length of staminate spikes was significantly larger for *A. littorum* than *A. occidentale* (20.6 versus 13.9 mm) (Table 1) and staminate spikes > 3 cm in length were commonly formed on male plants of *A. littorum*. In addition, the mean width of staminate spikes of *A. littorum* (3.4 mm) was significantly greater than the mean width of staminate spikes of *A. occidentale* (2.9 mm) (Table 1).

A major difference found between *A. littorum* and *A. occidentale* that has previously been unreported, was that *A. littorum* frequently develops staminate flowers with 5 petals, and rarely, flowers with 6 petals. Although *A. littorum* predominantly produced 4-merous staminate flowers, as reported by Hawksworth et al. (1992), it also produced 3-merous flowers, but less often than 5-merous flowers. A survey of 100 flowers in separate populations of *A. littorum* indicated that it produced about 15% 3-merous, 60% 4-merous, and 25% 5-merous flowers. Only one 6-merous flower was found during our survey of petal numbers and this configuration was only rarely observed while we were measuring morphological characters for staminate flowers. Staminate flowers of *A. occidentale* were predominantly 3- or 4-merous, but we did observe one 5-merous flower while measuring staminate flower dimensions; no 6-merous flowers were observed on staminate plants of *A. occidentale*. The relatively low frequency of 3-merous flowers and frequent formation of 5-merous flowers by *A. littorum* clearly distinguished it from *A. occidentale*. Furthermore, *A. littorum* consistently formed larger 3- and 4-merous flowers, with significantly longer and wider petals than *A. occidentale* (Table 1). *Arceuthobium littorum* also produced significantly larger anthers, some which were 1.5 mm in diameter (Table 1). The largest anther diameter measured for *A. occidentale* was 1 mm.

Although Hawksworth et al. (1992) reported that the fruits of *A. littorum* were slightly longer than those of *A. occidentale*, our measurements of mature fruits indicated they were approximately the same length (means and ranges), but that the average width of fruits of *A. littorum* was greater than for *A. occidentale* (Table 1). However, the largest fruits of *A. occidentale* measured were over 4.5 mm in width, while those of *A. littorum* did not exceed 4.4 mm. Therefore, the dimensions of mature fruits cannot be used to distinguish these dwarf mistletoes from each other, nor can the dimensions of mature seeds (Table 1). A clear distinction between the fruits of these two taxa was their color and whether they were glaucous or non-glaucous. Fruits of *A. littorum* were consistently dark green and sometimes red, but only lightly glaucous, if at all. In contrast, fruits of *A. occidentale* were light green and remarkably glaucous to the point of appearing blue. Removal of the waxy coating on the fruits of *A. occidentale* revealed their light green color, but the fruits of *A. littorum* were distinctly dark green and remained so when any wax on the fruit surface was removed.

Flowering of *A. littorum* started in late August, peaked in mid to late September, and ended by mid October. In contrast, *A. occicentale* did not start flowering until early October, peaked in late October or early November, and did not complete flowering until mid December. Fruit maturation of *A. littorum* also occurred earlier than for *A. occidentale*. Fruits of *A. littorum* started seed dispersal in early September, peaked in late September and early October, and completed this process by late October during 2010. However, we observed some seed dispersal in early November 2011 and Peirce (1905) reported that seeds of *A. littorum* (classified then as *A. occidentale*) were still dispersing around Christmas in 1903. Therefore, additional observations of seed dispersal of *A. littorum* are warranted to better define when it is completed. Seed dispersal of *A. occidentale* didn't start until early October, peaked in late October to early November, and consistently continued into December. Therefore, flowering and seed dispersal of *A. littorum* usually started approximately one month before *A. occidentale* and was completed about one month earlier, but as mentioned above, additional observations of seed dispersal are needed for *A. littorum* because of the report by Peirce (1905).

Another distinction between *A. littorum* and *A. occidentale* reported by Hawksworth et al. (1992) is that the former species consistently induces large, non-systemic witches' brooms on its pine hosts, while the latter species does not. We also observed this characteristic of broom formation on *Pinus muricata* and *P. radiata* by *A. littorum* and only rarely observed broom formation on *P. sabiniana* infected by *A. occidentale*. The reasons for the rare formation of witches' brooms on *P. sabiniana* remain unclear, but it is evidently related to a specific physiological interaction between *A. occidentale* and *P. sabiniana* because we observed that *A. occidentale* did induce the formation of brooms on its less frequently infected pine hosts such as *P. ponderosa* Dougl. ex Lawson & C. Lawson and *P. coulteri* D. Don.

Although the pine hosts of these dwarf mistletoes differ, little is known about host susceptibility because the distribution of *A. littorum* does not overlap with the distribution of the pines' hosts of *A. occidentale* and vice versa. Scharpf (1969) successfully inoculated *Pinus radiata* with *A. occidentale*, and this host-mistletoe combination has been reported from near Mount Hamilton, CA where ornamental *P. radiata* was planted near *P. sabiniana* infected with *A. occidentale* (Hawkworth and Wiens 1996). But the susceptibility of the pine hosts of *A. occidentale* to *A. littourm* remains unknown, as does the susceptibility of *P. muricata* to *A. occidentale*. Therefore, an artificial cross inoculation study using seeds of *A. littorum* on the hosts of *A. occidentale,* and vice versa, should provide useful information on the host specificity of these dwarf mistletoes.

CONCLUSIONS

Although these dwarf mistletoes were considered to be conspecific until 1992, there are several morphological and physiological characters that support their classification at the specific level (Table 2). While color is not generally considered a reliable character to use for distinguishing dwarf mistletoes, particularly in the United States (Hawksworth and Wiens 1996), these two taxa can easily be distinguished by plant color, even if the plants are distinctly glaucous or not (Table 2). Because the dimensions of female plants, mature fruits, and seeds were similar for these species, the characters of female plants are not useful for distinguishing between *A. littorum* and *A. occidentale*. The most reliable characters to use for distinguishing these species are associated with male plants. The staminate spikes of *A. littorum* are frequently unbranched and are often much longer (> 3 cm) and thicker than those of *A. occidentale* (Table 2). Furthermore, while both species produce 4-merous staminate flowers, *A. littorum* frequently produces 5-merous flowers (ca. 25%), 3-merous flowers occasionally (ca. 15%), and rarely forms 6-merous flowers (< 1%); whereas *A. occidentale* produces 3- and 4-merous flowers in approximately equal proportions, and very rarely forms 5-merous flowers. The frequent formation of 5-merous flowers by *A. littorum* clearly delimits it from *A. occidentale* and other dwarf mistletoes in California. The formation of 5-merous flowers has only been reported for *A. blumeri* A. Nelson from southern Arizona and northern Mexico and *A. strictum* from northern Mexico (Hawksworth and Wiens 1996). Another important difference between *A. littorum* and *A. occidentale* is that the flowers of *A. littorum* are significantly larger in diameter, have larger petals and larger anthers. The phenology of the two species also separates them because *A. littorum* flowers and disperses seed about one month earlier than *A. occidentale*. Therefore, we agree with Nickrent and Butler (1990), Hawksworth et al. (1992), and Hawksworth and Wiens (1996) that *A. littorum* and *A. occidenale* are distinct species and should continue to be recognized as such. These mistletoes are clearly defined by both morphological and physiological differences that support their classification at the specific rank.

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Table 1. Morphological measurements for *Arceuthobium littorum* and *A. occidentale.* Data are listed as **mean** (range) [n]. Means followed by different capital letters in the same row were significantly different (ANOVA followed by a Tukey's Honestly Significant Differences post hoc test, $\alpha \leq 0.05$). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements are in mm.

Character	*Arceuthobium littorum*	*Arceuthobium occidentale*
Plant Height		
Female	**10.3** A (5.1-18.7) [100a]	**10.6** A (4.9-23.2) [280a]
Male	**10.5** A (5.4-22.8) [a]	**10.1** A (4.7-24.1) [a]
Basal Diameter		
Female	**3.4** A (2.4-6.9) [a]	**3.2** B (1.7-6.0) [a]
Male	**3.5** A (2.5-5.8) [a]	**3.0** B (1.8-6.4) [a]
Length of Third Internode		
Female	**13.7** A (7.1-23.6) [a]	**12.0** B (4.6-20.6) [a]
Male	**13.5** A (6.9-19.6) [a]	**11.7** B (4.8-21.3) [a]
Width of Third Internode		
Female	**2.6** A (1.9-3.7) [a]	**2.2** B (1.3-3.5) [a]
Male	**2.7** A (1.8-3.6) [a]	**2.2** B (1.3-3.8) [a]
Staminate Spike Length	**20.6** A (6.1-55.9)[a]	**13.9** B (6.2-33.9) [200b]
Staminate Spike Width	**3.4** A (2.1-4.2) [a]	**2.9** B (2.2-4.1) [b]
Mean Flower Diameter		
3-merous	**3.5** A (2.2-4.8) [50]	**3.0** B (2.2-4.1) [185c]
4-merous	**5.2** A (3.4-6.9) [135]	**4.1** B (3.0-6.2) [c]
5-merous	**5.7** (4.6-7.0) [20]	Only one 5-merous flower observed
Perianth Length	**1.9** A (1.0-2.8) [205b]	**1.5** B (1.1-2.5) [370d]
Perianth Width	**1.6** A (0.8-2.5) [b]	**1.3** B (0.7-2.2) [d]
Anther Diameter	**0.9** A (0.4-1.5) [b]	**0.6** B (0.4-1.0) [d]
Anther Distance from Tip	**0.9** A (0.4-1.7) [b]	**0.6** B (0.2-1.2) [d]
Mean Fruit Length	**5.3** A (4.1-6.4) [a]	**5.2** A (3.9-6.8) [220e]
Mean Fruit Width	**3.6** A (2.9-4.4) [a]	**3.3** B (2.4-4.7) [e]
Seed Length	**3.4** A (2.5-4.2) [a]	**3.4** A (2.5-4.3) [e]
Seed Width	**1.3** A (1.0-1.6) [a]	**1.3** A (1.0-1.7) [e]

Table 2. Principal morphological and physiological characteristics distinguishing *Arceuthobium littorum* from *Arceuthobium occidentale*. Numerical values are means, except staminate spike length.

Character	*Arceuthobium littorum*	*Arceuthobium occidentale*
Basal Diameter[a] (mm)	3.5	3.1
Plant Color	Brown-green, dark green, yellow-brown	Yellow, yellow-green, straw
Plants Glaucous	Rarely	Usually
Staminate Spike Length	Frequently > 3 cm	Usually < 3 cm
Staminate Spike Width (mm)	3.5	2.9
Flower Diameter (mm)		
3-merous	3.5	3.0
4-merous	5.2	4.1
5-merous	5.7	- [b]
Flowers with 3 petals	Occasional	Common
Flowers with 5 petals	Common	Rare
Flowers with 6 petals	Rare	None observed
Perianth Length (mm)	2.0	1.5
Perianth Width (mm)	1.6	1.3
Anther Diameter (mm)	0.9	0.6
Anther Distance from Tip (mm)	0.9	0.6
Fruit Color	Dark green to red	Light green
Fruits Glaucous	Lightly glaucous	Highly glaucous

[a] – Male and female plants combined.
[b] – Only one 5-merous flower observed.

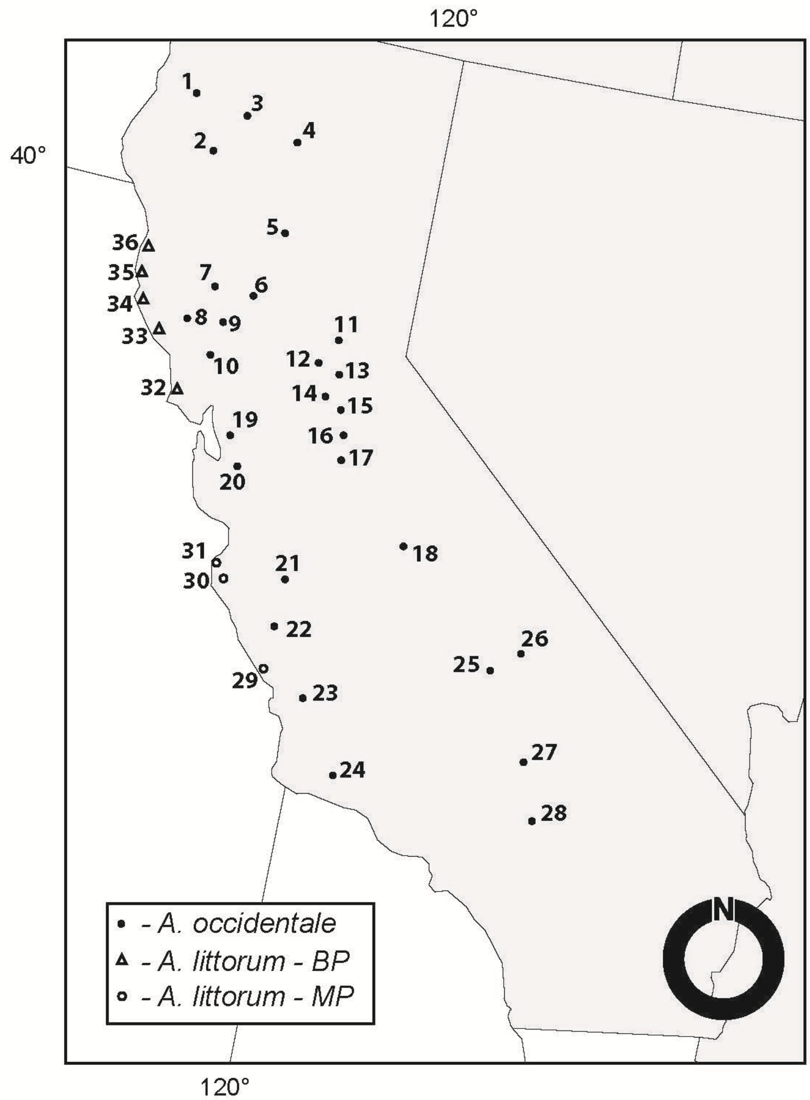

Figure 1. Approximate location of collection sites in California. Dark circles represent locations where *A. occidentale* was collected and measured on *Pinus sabiniana*. Open circles represent locations where *A.littorum* was collected and measured on *Pinus radiata* (MP). Open triangles represent locations where *A. littorum* was collected and measured on *Pinus muricata* (BP). Numbers correspond to the following locations: 1 – 2 km S of St. Rte. 299 on Burnt Ranch School rd.; 2 – Beegum Creek on St. Rte. 36; 3 – 1 km S of St. Rte. 299 on Carr Powerhouse rd.; 4 – 29 km E. of Redding on St. Rte. 44 at Black Butte rd.; 5 – 14 km NE of St. Rte. 99 on St. Rte. 70; 6 – 0.5 km E of Colusa County line on St. Rte. 20; 7 – 3 km from St. Rte. 20 on County Rd. M-12; 8 –3 km S of Covelo on St. Rte. 162; 9 – Entrance to Langtry Winery; 10 – Butts Canyon; 11 – 1 km S of Auburn on St. Rte. 49; 12 – Beales Pt. Campground on Folsom Lake; 13 – 4 km N of Placerville on St. Rte. 49; 14 – 6 km S of St. Rte. 16 on St. Rte. 124; 15 – Columbia Airport rd.; 16 – 11 km S of Angels Camp on St. Rte. 4; 17 – N side of Roberts Memorial Bridge on St. Rte. 120; 18 – 0.2 km SW of Prather on Auberry Rd.; 19 – 3 km N of entrance gate to Mount Diablo State Park; 20 – 19 km E of San Jose on Mount Hamilton rd.; 21– 5 km W of visitors center in Pinnacles Nat. Mon.; 22 – 10 km E of Jolon on Naciemento-Ferguson rd.; 23 – 5 km SE of St. Rte. 58 on Pozo rd.; 24 – 13 km E of Los Olivos on Figueroa Mt. rd.; 25 – 13 km E of Glenville on St. Rte. 155; 26 – 3 km S of Kernville; 27 – 1 km SW of St. Rte. 58 on Hart Flat rd.; 28 – 1 km S of Lake Hughes on Lake Hughes rd; 29 – 1 km N of Cambria on Santa Rosa Cemetery rd.; 30 – 0.5 km E of St. Rte. 1 on Fern Canyon rd.; 31 – Pacific Grove, 0.5 km E of Stevenson Dr. on Forest Lake rd.; 32 – 3 km NW of Inverness, Pt. Reyes Nat. Seashore; 33 – 0.5 km E of St. Rte. 1 on Kruse-Rhododendron rd.; 34 – 7 km E of Pt. Arena on Eureka Hill rd.; 35 – 4 km E of Albion River on Little River rd.; 36 – 4 km E of Fort Bragg on St. Rte 20.