# *ARCEUTHOBIUM TSUGENSE* (VISCACEAE): FOUR SUBSPECIES WITH CONTRASTING MORPHOLOGIES AND HOST DISTRIBUTIONS

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## ABSTRACT

There have been four subspecies of hemlock dwarf mistletoe (*Arceuthobium tsugense*: Viscaceae) described by various investigators of this complex group of parasitic flowering plants: subsp. *tsugense*, subsp. *amabilae*, subsp. *contortae*, and subsp. *mertensianae*. As suggested by their subspecific epithets, these taxa differ in their host affinities; parasitizing different and the same hosts to varying degrees. Although these taxa also have morphological differences, their classification has been under debate for many years. Therefore, we compared the morphological characteristics of each subspecies using both univariate and multivariate statistical analyses in order to better assess their differences. Because some investigators have grouped hemlock dwarf mistletoe with western dwarf mistletoe (*A. campylopodum*), we also compared the subspecies of hemlock dwarf mistletoe with western dwarf mistletoe. Our morphometric analyses demonstrated that all of the subspecies are morphologically distinct from western dwarf mistletoe and that subsp. *contortae* is the most morphologically differentiated of the subspecies. Overlap in the morphological characters across two of the other three subspecies was evident; yet, subsp. *amabilae* and subsp. *mertensianae* were also consistently delimited using female and male plant morphologies. Statistical comparisons of female or male plants via standard and stepwise discriminant function analyses demonstrated that without consideration of host plant, female and male *A. tsugense* subsp. *tsugense* are morphologically similar to corresponding plants of subsp. *amabilae* and *mertensianae* but not subsp. *contortae* or *A. campylopodum*.

Key Words: hemlock dwarf mistletoe, *Arceuthobium*, mountain hemlock, noble fir, Pacific silver fir, western hemlock

## RESUMEN

Ha habido cuatro subespecies de muérdago enano (*Arceuthobium tsugense*: Viscaceae) descritos por varios investigadores en este grupo complejo de angiospermas parásitas: subsp. *tsugense*, subsp. *amabilae*, subsp. *contortae*, and subsp. *mertensianae*. Como se sugiere por sus epítetos subespecíficos, estos taxa difieren en sus afinidades por los huéspedes; parasitando diferentes y el mismo huésped en varios grados. Aunque estos taxa también tienen diferencias morfológicas, su clasificación ha estado en debate durante muchos años. Sin embargo, hemos comparado las características morfológicas de cada subespecie usando análisis estadísticos tanto univariantes como multivariantes para evaluar mejor sus diferencias. Como algunos investigadores han agrupado este muérdago enano con otro muérdago enano del oeste (*A. campylopodum*), nosotros también comparamos las subespecies de ambos muérdagos. Nuestro análisis morfométrico demostró que todas las subespecies son distintas morfológicamente del muérdago enano del oeste y que la subsp. *contortae* es la más diferenciada morfológicamente de las subespecies. El solapamiento en los caracteres morfológicos entre dos de las otras tres subespecies fue evidente; aunque, subsp. *amabilae* y subsp. *mertensianae* fueron también delimitadas consistentemente usando morfologías de plantas masculinas y femeninas. Las comparaciones estadísticas de plantas masculinas o femeninas mediante análisis de función discriminante standard y aumentada demostró que sin consideración de la planta huésped, los ejemplares masculinos y femeninos de *A. tsugense* subsp. *tsugense* son similares morfológicamente a las plantas correspondientes a las subsp. *amabilae* y *mertensianae* pero no a la subsp. *contortae* o *A. campylopodum*.

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosend.) G.N. Jones, Viscaceae) is a damaging parasite of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) from central California to southeastern Alaska (Smith 1969; Hawksworth & Wiens 1996; Muir & Hennon 2007). Severe infection of western hemlocks has been shown to be associated with reduced growth, premature mortality, and the formation of trunk cankers which provide entrance courts for a variety of wood decay fungi (Weir 1916; Wellwood 1956; Smith 1969; Etheridge 1973; Hennon et al. 2001; Muir & Hennon 2007). Infection also can result in branch cankers and mortality caused by at least three species of fungi in noble fir (*Abies procera* Rehder) and Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) in central Oregon (Filip et al. 1979). Hemlock dwarf mistletoe is also important from an ecological perspective in that it creates structural diversity and provides habitat for a variety of wildlife species (Mathiasen 1996, Muir & Hennon 2007). Although the dwarf mistletoe populations parasitizing western hemlock as well as mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), Pacific silver fir, noble fir and shore pine (*Pinus*

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*contorta* Douglas ex Loudon subsp. *contorta*) in California, Oregon, Washington, and British Columbia have been recognized as *A. tsugense* by many investigators, there remains ongoing debate regarding the taxonomic treatment of these dwarf mistletoe populations (Gill 1935; Hawksworth 1987; Hawksworth & Wiens 1972, 1996; Nickrent et al. 2004; Nickrent 2012, 2016; Mathiasen & Kenaley 2015b).

In 1903, R.O. Rosendahl first recognized that the dwarf mistletoe populations parasitizing western hemlock were morphologically distinct from *Arceuthobium campylopodum* Engelm. Rosendahl classified the dwarf mistletoe on western hemlock as a species of *Razoumofskya* Hoffman because at that time most American botanists followed the American Code which preserved the use of *Razoumofskya* over *Arceuthobium* M. Bieberstein. Thereafter, in 1930, the Cambridge Botanical Congress voted to conserve *Arceuthobium* over *Razoumofskya* and most American plant taxonomists then accepted the use of *Arceuthobium*. In the first monograph for *Arceuthobium*, Gill (1935) acknowledged the host susceptibility differences exhibited by different dwarf mistletoes in the United States and treated hemlock dwarf mistletoe as a host-form of *A. campylopodum*: forma *tsugensis* (Rosend.) Gill which infected western and mountain hemlocks. In 1936, G. N. Jones rejected Gill's host-form concept and recombined *Razoumofskya tsugensis* Rosend. as *Arceuthobium tsugensis* (Rosend.) G.N. Jones.

In their first monograph for *Arceuthobium*, Hawksworth and Wiens (1972) rejected Gill's host-form concept and, hence, retained the classification of hemlock dwarf mistletoe as *Arceuthobium tsugense* rather than *A. tsugensis*. Thereafter, Hawksworth (1987) summarized the taxonomy of *A. tsugense* and, according to principal host, separated this species into three different races: the western hemlock, mountain hemlock, and shore pine races. Hawksworth et al. (1992) presented another interpretation for the classification of *A. tsugense*; wherein, they described the western hemlock and mountain hemlock races proposed by Hawksworth (1987) as subspecies of *A. tsugense*: western hemlock dwarf mistletoe—*A. tsugense* subsp. *tsugense* and mountain hemlock dwarf mistletoe—*A. tsugense* (Rosend.) G.N. Jones subsp. *mertensianae* Hawksworth & Nickrent, while maintaining the dwarf mistletoe parasitizing shore pine as a race of subsp. *tsugense*. The classification of subsp. *mertensianae* was supported by isozyme analysis, but the separation of the shore pine race as a separate taxon was not (Nickrent & Stell 1990).

In a revision of their monograph of *Arceuthobium*, Hawksworth and Wiens (1996) maintained the classification of *A. tsugense* as proposed by Hawksworth et al. (1992). Wass and Mathiasen (2003) provided further detailed study of the morphology, phenology, and host range of the race of *A. tsugense* parasitizing shore pine in southern British Columbia and northwestern Washington, and concluded that shore pine dwarf mistletoe should be recognized as a subspecies—*A. tsugense* (Rosend.) G.N. Jones subsp. *contortae* Wass & Mathiasen. Likewise, Mathiasen and Daugherty (2007) examined the morphology and host ranges of the *A. tsugense* populations severely parasitizing Pacific silver fir, noble fir, and mountain hemlock from southern to northern Oregon and classified these plants as *A. tsugense* (Rosend.) G.N. Jones subsp. *amabilae* Mathiasen & C. Daugherty. Presently, we follow the classification of *A. tsugense* consisting of the four subspecies as described above, since a combination of host range, plant height, flower diameter, fruit dimensions, and/or, to a lesser extent, phenological differences in flowering and seed dispersal delimit these subspecies of *A. tsugense*.

Recent taxonomic treatments for *Arceuthobium*, however, have either subsumed *A. tsugense* under *A. campylopodum* (Kuijt 2012) or recombined *A. tsugense* as a subspecies of *A. campylopodum* (Nickrent 2012, 2016). The aforementioned treatments have since created a dilemma for botanists and foresters who work with these parasitic plants because there are now multiple modern classifications of the dwarf mistletoes parasitizing hemlocks, true firs, and shore pine in the Pacific Northwest and Canada. Because of these varying interpretations of the taxonomic status of hemlock dwarf mistletoe and since no study to date has directly compared the morphologies of the four subspecies of *A. tsugense* we recognize as valid taxa, we conducted this study to determine if these subspecies can be distinguished based on morphologic analyses performed using univariate and multivariate statistics. We also summarized host susceptibility data for the subspecies from several previous studies of their host ranges. Because the treatments by Kuijt (2012) and Nickrent (2012, 2016) suggested that *A. tsugense* and its allied subspecies are morphologically and/or genetically indistinguishable from western dwarf mistletoe, we also compared male and female morphologies of the subspecies of *A. tsugense* separately with those of *A. campylopodum*.

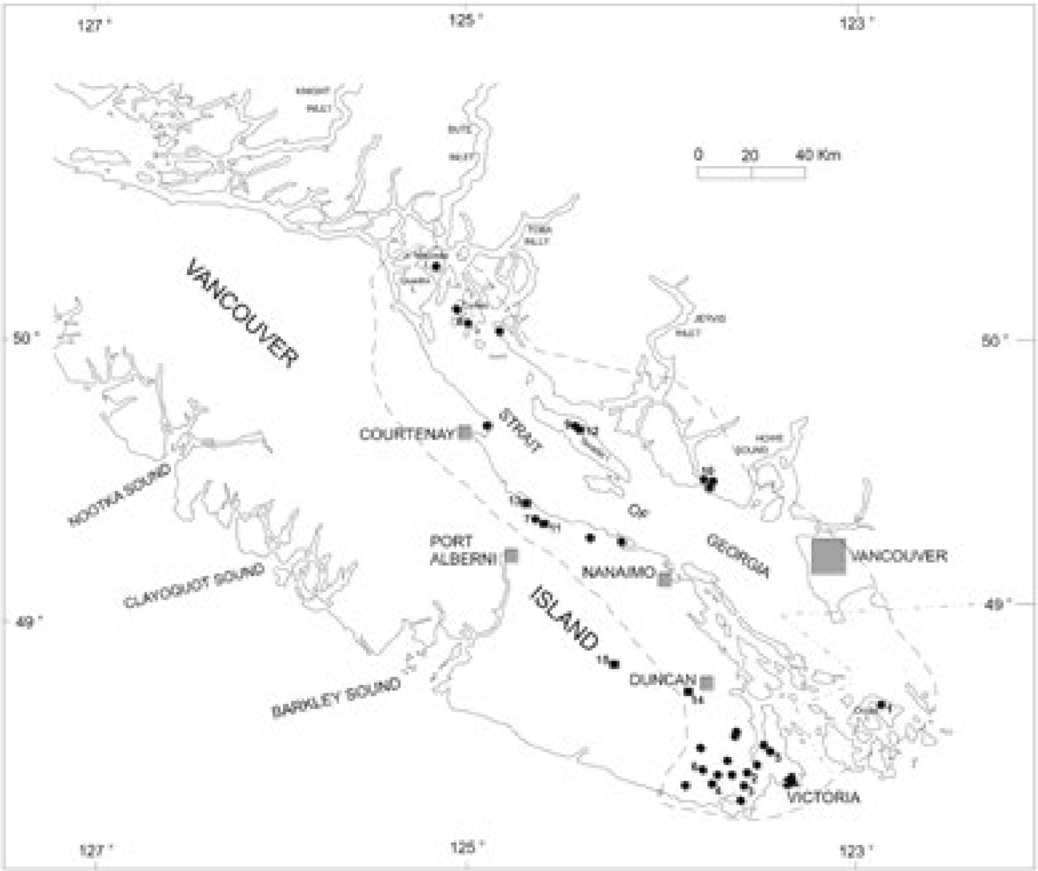


**Fig. 1. Dashed line encloses the distribution of *Arceuthobium tsugense* subsp. *contortae*. Black circles indicate known populations and numbered circles indicate populations sampled for morphological measurements and host susceptibility: Washington: 1—Orcas Island; British Columbia: 2—Mount Wells, 3—Mount Helmcken, 4—Bluff Mountain, 5—Mount Work, 6—Trap Mountain, 7—Spider Lake, 8—Cortes Island, 9—Texada Island, 10—Sechelt. Black squares indicate populations of *Arceuthobium tsugense* subsp. *tsugense* sampled for morphological measurements and host susceptibility: British Columbia: 11—Spider Lake, 12—Texada Island, 13—Bowser, 14—Holt Creek, 15—Caycuse Summit. (From Wass & Mathiasen 2003).**

## METHODS

Morphological data for 19 populations of *Arceuthobium tsugense* distributed throughout most of its geographic range on *Tsuga heterophylla* in the United States and on Vancouver Island, British Columbia were collected by Wass and Mathiasen (2003)(Figs. 1 and 2). They also sampled ten *A. tsugense* subsp. *contortae* populations scattered throughout its principal range in British Columbia and on Orcas Island, Washington (Fig. 1). A total of 16 populations of *A. tsugense* subsp. *amabilae* were sampled from within its geographic range in Oregon (Mathiasen & Daugherty 2007) (Fig. 3). In order to make a comparison with the morphological characters of *A. tsugense* subsp. *mertensianae*, a total of 14 populations of subsp. *mertensianae* were sampled from central and northern California as well as southern Oregon (Mathiasen & Daugherty 2007) (Fig. 3). We collected morphological data for *A. campylopodum* from 60 populations (30 each from ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) and Jeffrey pine (*P. jeffreyi* Grev. & Balfour) from throughout most of its geographic range (Mathiasen & Kenaley 2015a) (Fig. 4). From each population, 20 to 40 infections were collected and the dominant shoot from each infection was used for morphological measurements. The subsp. *tsugense* populations had 10 female and 10 male infections sampled from each population. Voucher specimens of *A.*

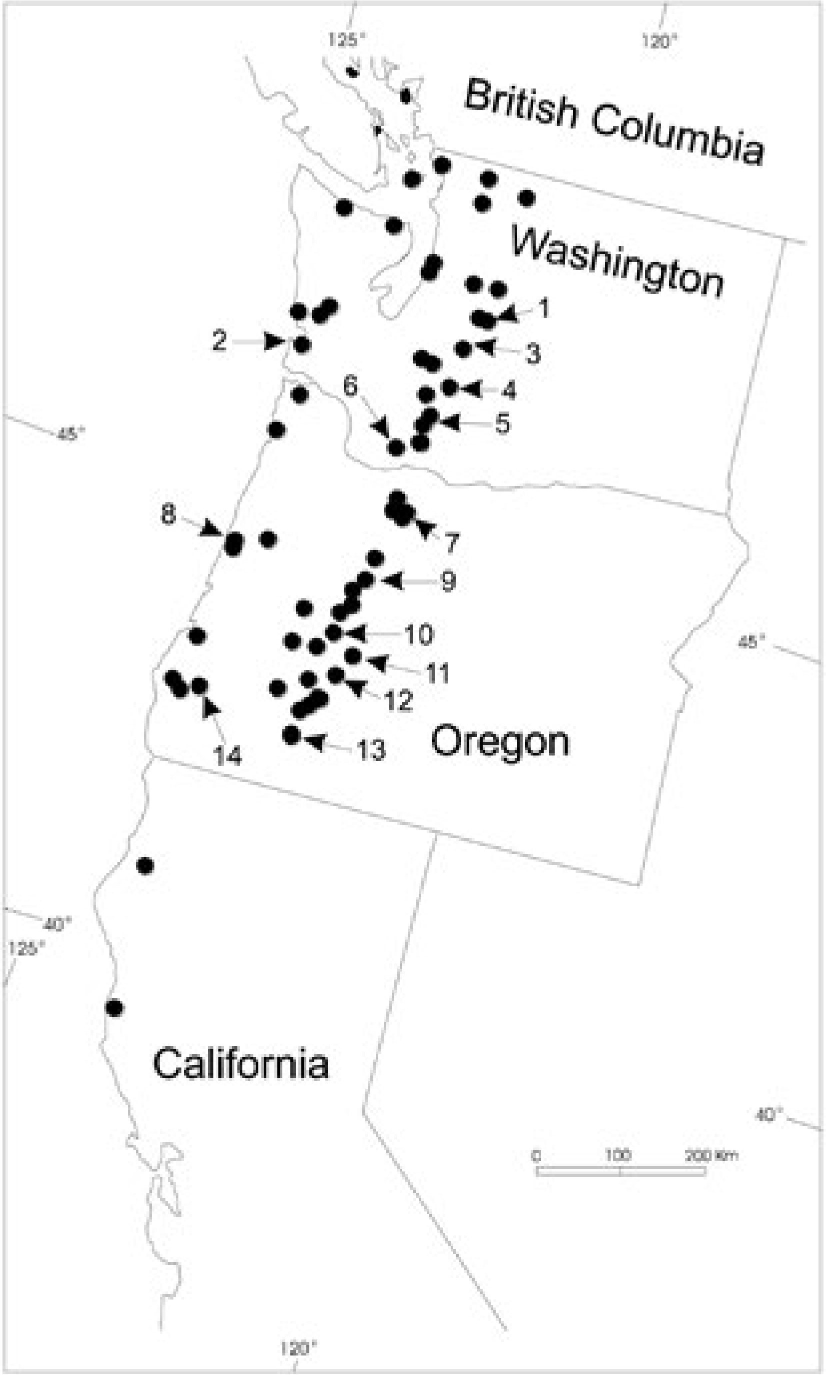


**Fig. 2. Distribution of *Arceuthobium tsugense* subsp. *tsugense* in Washington, Oregon and California (Hawksworth and Wiens, 1996). Black circles indicate known populations and numbered circles indicate populations where morphological data were collected. Washington: 1—Snoqualmie Pass, 2—Westport, 3—Huckleberry Creek, 4—Cortright Creek, 5—Clearwater Creek, 6—Wind River Experimental Forest; Oregon: 7—Wapinitia Pass, 8—Desolation Saddle; 9—Huckleberry Creek, 10—Indigo Spring; 11—Wall Creek, 12—Calapooya Ridge, 13—Union Creek, 14—Iron Mountain. (From Wass & Mathiasen 2003).**

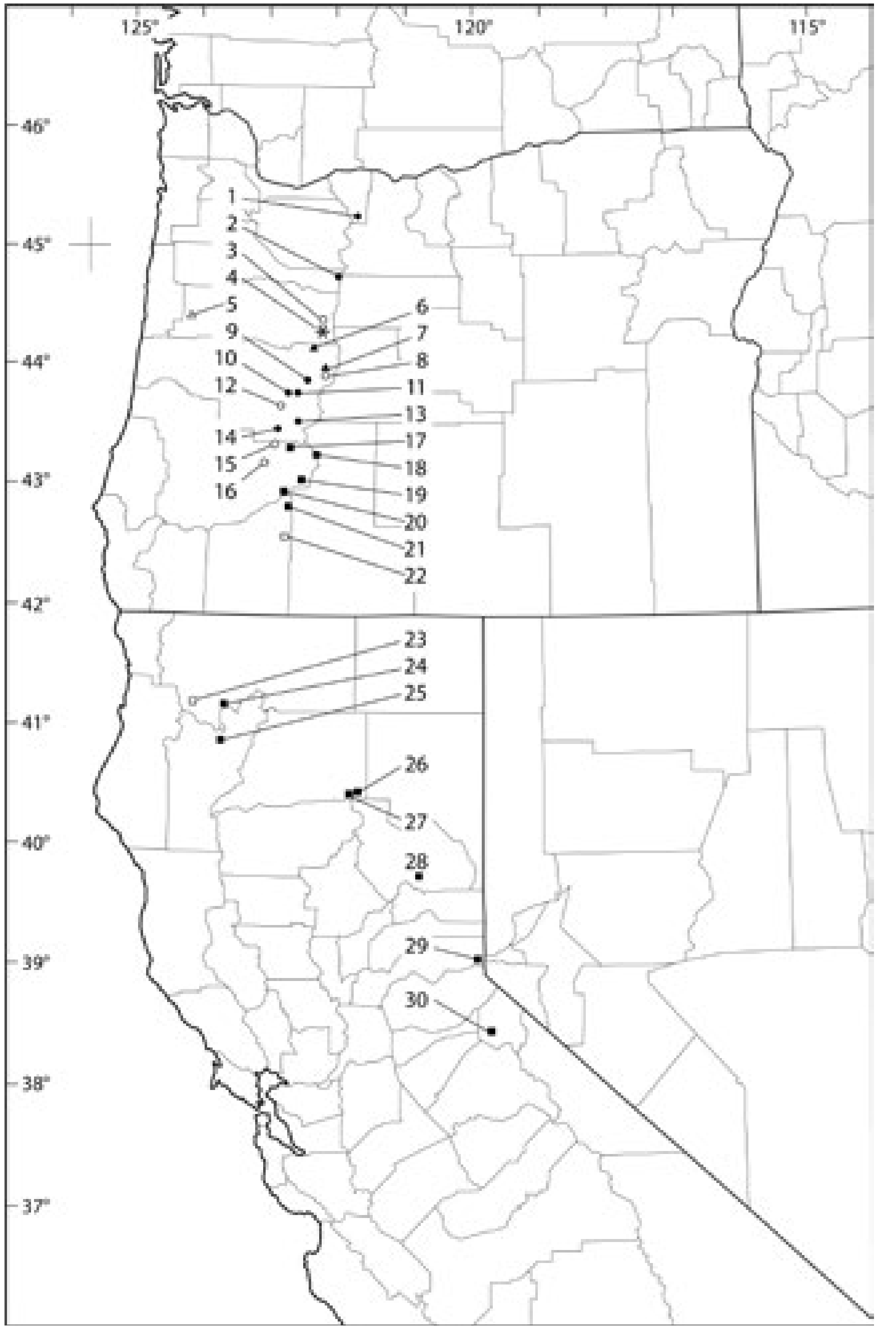


**Fig. 3.** Approximate locations of populations sampled for *Arceuthobium tsugense* subsp *amabilae* and *A. tsugense* subsp. *mertensianae* in Oregon and California. Numbers 1–16 represent subsp. *amabilae* and numbers 17–30 represent populations of subsp. *mertensianae*. OREGON: **1**—Bennett Pass; **2**—Skyline Road, **3**—Wildcat Mountain, **4**—Bunchgrass Mountain, **5**—Mary's Peak, **6**—Frissell Point, **7**—Olallie Ridge, **8**—Pat Saddle, **9**—Lowell Mountain, **10**—Huckleberry Mountain, **11**—Blair Lake, **12**—Holland Meadow, **13**—Hemlock Butte, **14**—Warner Mountain, **15**—Staley Ridge, **16**—Snowbird Camp, **17**—Calapooya Ridge, **18**—Windigo Pass, **19**—Mount Thielsen Trail, **20**—Beaver Meadow on State Route 230, **21**—Huckleberry Campground, **22**—Mount McLaughlin Trail; CALIFORNIA: **23**—Chimney Rock, **24**—Eaton Lake, **25**—Snowslide Lake, **26**—Kings Creek, **27**—Diamond Peak, **28**—Long Lake, **29**—Alpine Meadows Ski Area, **30**—Mosquito Lakes. (From Mathiasen & Daugherty 2007).

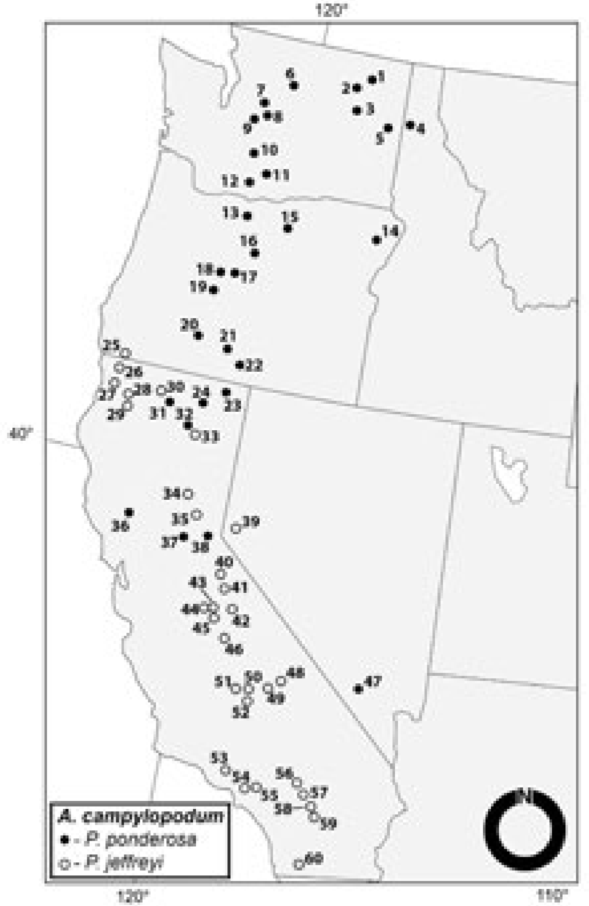


Fig. 4. Approximate locations of collection sites for *Arceuthobium campylopdum* in Washington, Idaho, Oregon, California, and Nevada. Closed circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. Numbers correspond to the following locations: Washington: **1**—4.5 km N of Gifford on St. Rte. 25, **2**—20 km S of Fruitland on St. Rte. 25, **3**—2 km NW of Nespelem on St. Rte. 155, **5**—16 km S of Spokane on St. Rte. 195, **6**—2.5 km W of St. Rte. 153 on Squaw Creek rd., **7**—Lake Wenatchee on Chiwawa River Loop rd., **8**—2.6 km W of Squilchuck St. Park on road to Mission Ridge Ski Area, **9**—0.8 km W of St. Rte. 97 on St. Rte 970, **10**—17.6 km E of White Pass on St. Rte. 12, **11**—2 km N of Satus Pass on St. Rte. 97, **12**—3 km S of Trout Lake on St. Rte. 141; Idaho: **4**—2.3 km N of Coeur d'Alene on Fernan Lake rd.; Oregon: **13**—6.4 km W of Friend on forest rd. 27, **14**—6.4 km S of Joseph on E shore of Wallowa Lk., **15**—9.4 km on Sheep Cr. rd from forest rd. 51, Wallowa-Whitman Nat. For., **16**—1.8 km E of Ochoco Summit on St. Rte. 26, **17**—12.2 km W of St. Rte. 97 on St. Rte. 138, **18**—15.2 km S of Sisters on forest rd. 16, **19**—1 km from forest rd. 44 on forest rd. 4410, Pringle Falls Exp. For., **20**—Fort Klamath Cemetery on St. Rte. 62, **21**—3 km W of Quartz Mtn. Pass on St. Rte. 140, **22**—Warner Mtn. Ski Hill on St. Rte. 26, **25**—6 km S of Takilma on Greyback rd.; California: **23**—3.4 km W of County rd. 48 on forest rd. 73, west shore of Goose Lk., **24**—16 km N of Adin on St. Rte. 299/139, **26**—1 km S of forest rd. 17N26 on forest rd. 17N11, Klamath Nat. For., **27**—6.2 km W of St. Rte. 96 on Dillon Mtn. rd., **28**—9.6 km S of Callahan on St. Rte. 3, **29**—10 km E of St. Rte 3 on forest rd. 17, Shasta-Trinity Nat. For., **30**—2.4 km W of Stewart Hot Springs on forest rd. 17, **31**—2 km N of St. Rte. 89 on Mt. Shasta Ski Park rd., **32**—0.1 km S of St. Rte. 299 on St. Rte. 89, **33**—2 km S of Old Station on St. Rte. 44, **34**—2 km W of St. Rte. 44 on forest rd. 101, **35**—14.4 km W of Susanville on St. Rte. 36, **36**—19.5 km N of Upper Lake on Pillsbury Lk. rd., **37**—7.7 km N of Pollock Pines on forest rd. 4, **38**—at entrance to Sugar Pine State Park, west shore of Lk. Tahoe, **40**—1 km N of Markleeville on St. Rte. 89, **41**—Silver Creek Campground on St. Rte. 4, **42**—Column of the Giants on St. Rte. 108, **43**—Pinecrest Transfer Station 0.5 km W of Pinecrest on St. Rte. 108, **44**—1 km W of Long Barn on St. Rte. 108, **45**—8.5 km E of Crane Flat on St. Rte. 120, **46**—2 km W of Big Creek on rd. to Shaver Lk., **48**—8.5 km W of Sherman Pass on forest rd. 22S05, **49**—2.2 km S of Troy Mdws. Campground, Sequoia Nat. For., **50**—5.8 km N of rd. to Johnsonville on Western Divide Highway, **51**—Pine Flat, Sequoia Nat. For., **52**—Tiger Flat, Sequoia Nat. For., **53**—6.2 km S of St. Rte. 33 on rd. to Mt. Reyes, **54**—1.4 km W of Cloud Burst on St. Rte. 2, **55**—1 km W of Big Pines on St. Rte. 2, **56**—2.4 km N of Fawnskin on forest rd. 2N71, **57**—1.9 km from St. Rte. 38 on rd. to Jenks Lk., **58**—near Ranger Station in Idylwild, **59**—1.1 km S of the S Fork San Jacinto River Bridge on St. Rte. 74, **60**—0.5 km S of Horse Heaven Campground on Sunrise Highway; Nevada: **39**—Bowers Mansion St. Park, **47**—4.1 km W of Ranger Station at Old Ski Tow Historic Site, Kyle Canyon. (From Mathiasen & Kenaley 2015a).

*campylopodum*, *A. tsugense* subsp. *amabilae*, and subsp. *mertensianae* consisting of the mistletoe with host material were deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or the University of Arizona Herbarium, Tucson (ARIZ). Voucher and specific population data, including collection dates and GPS coordinates were also electronically archived via the Southwest Environmental Information Network (SEINet: http://swbiodiversity.org/seinet/). Voucher specimens of *A. tsugense* subsp. *tsugense* and subsp. *contortae* were deposited at the Pacific Research Centre, Canadian Department of Forestry, Victoria, B. C., Canada (DAVFP).

We sampled the dominant plant from each infection collected from principal hosts to standardize measurements across populations and taxa. Morphologic characters measured were those most commonly used for the taxonomic classification of *Arceuthobium* (Hawksworth & Wiens 1996; Wass & Mathiasen 2003; Mathiasen & Daugherty 2007; Mathiasen & Kenaley 2015a, 2015b, 2016), including: 1) plant height, basal diameter, length and width of the third internode, and shoot (plant) color; 2) mature fruit length, width, and color; 3) seed length, width, and color; 4) staminate spikes length and width; 5) staminate flower diameters for three- and four-merous flowers; 6) length and width of staminate flower petals; and, 7) anther diameter and distance to the petal tip (hereafter, referred to anther distance to tip). Plants were consistently measured within 12-h and rarely later than 24-h after collection. Only plants that were still attached to their host's branch and fully turgid were measured.

Measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7× magnifier equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ); both of which allowed accurate measurements to the nearest 0.1 mm. The basal diameter of plants was measured at the point where the plant was attached to the host branch. The length and width of the third internode distal to the base of plants were also included in our morphological analyses because these characters frequently have been reported for male and female plants of dwarf mistletoes and provide relative information on plant size and, most importantly, plant thickness (Hawksworth & Wiens 1972, 1996; Mathiasen & Daugherty 2007, 2009, 2013; Mathiasen & Kenaley 2015a, 2015b; Mathiasen et al. 2016; Kenaley et al. 2016). However, we were aware of Kuijt's (1969) study which demonstrated that plants of *Arceuthobium americanum* Nutt. ex Engelm.—and probably other large dwarf mistletoes—have intercalary meristems that permit continued elongation of the third internode over several years. Thus, to compensate for such variation among plants/taxa, we standardized the measurement of the third internode by measuring dominant plants at approximately the same time annually (male and female plants in July–August or August–September respectively) and determined the length and width with a digital caliper to the nearest 0.1 mm. The length of the third internode was determined by measuring between the apical-most portion of the second and third internodes distal to the base of a plant—locations (i.e. morphological "landmarks") along the plant length that are easily observed (see Figs. 2.1, 2.3, and 2.9 in Hawksworth & Wiens 1996). The width of the third internode was measured across its widest axis. Staminate spike and flower measurements were made during the peak of anthesis (July to August) and, likewise, fruit and seed measurements were made during peak seed dispersal (September to October). Measurements of staminate spike lengths and widths, flower dimensions, and fruit/seed dimensions were made to the nearest 0.1 mm with the 7x magnifier. Measurements of flower diameters of 3- and 4-merous staminate flowers for *A. tsugense* subsp. *contortae* were not distinguished from each other, but recorded as one flower diameter regardless of the number of petals (Wass & Mathiasen 2003). However, the measurements of 3- and 4-merous flowers of all the other taxa were distinguished as separate measurements. Sample sizes for most morphological characters measured varied among the five taxa examined herein because of the number of populations sampled and the number of plants measured per population also varied.

### Statistical Analyses

Variance across individual female and male plant characters among *Arceuthobium campylopodum* and *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae*, and *tsugense* were examined via one-way analysis of variance (1-way ANOVA). Mean differences by plant character among taxa were determined separately using a post-hoc Tukey's honestly significant difference (HSD; $\alpha = 0.05$) test. Because the four subspecies of *A. tsugense* have been reclassified as or under *A. campylopodum* (Kuijt 2012; Nickrent 2012, 2016), we also executed separate Dunnett's tests to compare simultaneously individual female and male characters of *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae*, and *tsugense* alone to *A. campylopodum* (control). Complete morphologic records were then partitioned by plant sex and three multivariate analyses—multivariate analysis of variance (MANOVA) as well as standard (full-model) and stepwise quadratic discriminant function analyses (DFA; Quinn & Keough 2002)—were performed to assess whether significant differences existed among the combined morphologies of female or male plants across the subspecies of *A. tsugense* and with *A. campylopodum*. Morphological datasets were partitioned to either female or male plants in order to control for family-wise Type I error (Rancher 2002). Standard and stepwise quadratic DFAs compared actual taxonomic membership defined a priori via field determination to predicted taxonomic membership according to only female or male morphologies. Standardized correlation coefficients (SCC) for each female and male morphological character were calculated as part of the standard DFAs for female and male plants to delimit the principal morphologies contributing most to the discriminant function and, hence, separating the dwarf mistletoe taxa. Full-model DFAs were also validated by resampling separately the original (complete) data set for female and male plants; selecting at random 50 complete records per taxon and re-executing the DFA using a full-model (i.e., 8 female or 10 male characters). Female and male stepwise DFAs involved the sequential addition of morphological characters with the greatest-to-lowest absolute SCC to determine systematically the smallest number of morphological characters, female or male, resulting in the highest precision in taxonomic classification (%, predicted/field determined). All DFA models, either standard or stepwise, incorporated a prior probability per taxon (0.2), providing equal weight to taxon membership across taxa rather than sample size per taxon according to field determination. The diameter of staminate flowers was not included in the DFAs to avoid sampling bias as the ratio of 3- and 4-lobed male flowers differed by taxon. One-way and multivariate analyses of variances, multiple comparisons of mean differences, and DFAs were computed in JMP Pro v12.0.1 (SAS Institute, Cary, North Carolina, USA). Ninety-five percent (95%) confidence intervals ($\alpha = 0.05$) were also calculated to demonstrate variation in and approximate mean differences among plant characteristics among the subspecies of *A. tsugense* and *A. campylopodum*.

### Host Susceptibility Based on Natural Infection

Several studies have quantified the relative susceptibility of conifers to the subspecies of *Arceuthobium tsugense* using temporary circular plots with a six m radius (0.012 ha) placed around severely infected principal hosts of each of the subspecies, and herein, we summarized this information as it is relevant to species classification, identification, and management of these dwarf mistletoes (Mathiasen & Daugherty 2005, 2007; Muir & Hennon 2007). Live trees in each plot taller than 1.37 m (breast height) or larger than five cm in diameter at breast height were examined for dwarf mistletoe infection and the species and dwarf mistletoe rating (DMR, Hawksworth 1977) recorded for each tree. In most plots, the diameter of lives trees at breast height was also recorded to the nearest cm or nearest five cm. The number of plots established at study sites varied depending on the number of large, severely infected principal hosts present, but an attempt was made to complete at least 10 plots at each site. Based on this natural infection data, trees could be placed into susceptibility classes using the system developed by Hawksworth and Wiens (1972, 1996), which categorizes hosts as principal (90–100% infection), secondary (50–90% infection), occasional (5–50% infection), rare (> 0%, but less than 5% infection), and immune (0% infection) based on the percentage of trees infected growing within six m of severely infected principal hosts. In addition, mean DMR values were calculated for each species because mean DMR provided another estimate of the relative susceptibility of conifers to dwarf mistletoe infection.

Mathiasen and Hawksworth (1988) estimated the natural susceptibility of western hemlock and western white pine (*Pinus monticola* Douglas) to *Arceuthobium tsugense* subsp. *tsugense* using temporary circular plots around severely infected western hemlocks (DMR 5 or 6). Ten plots were completed at each of five sites near Union Creek, Oregon. In each plot, all live trees taller than breast height were examined for mistletoe infection and the species, diameter at breast height (DBH) to the nearest five cm, and DMR recorded. A total of 612 western hemlocks and 391 western white pines were sampled in 50 plots. In addition, they also sampled three sites in northern California and seven in southern Oregon where mountain hemlock was severely infected by subsp. *mertensianae*. They completed a total of 90 plots around severely infected mountain hemlocks (DMR 5 or 6) and again each live tree in a plot taller than breast height was examined and the same data recorded for each live tree (species, DBH, and DMR). They sampled a total of 469 mountain hemlocks and 343 western white pines.

In order to determine the susceptibility of shore pine and western hemlock to *Arceuthobium tsugense* subsp. *contortae* and *A. tsugense* subsp. *tsugense* based on natural infection in British Columbia, 173 temporary plots were established around large, severely infected residual trees (western hemlock or shore pine) at 10 locations (Wass & Mathiasen 2003) (Fig. 1). In each plot, trees taller than breast height were sampled and the species and DMR were recorded for each live tree. Similarly, Mathiasen and Daugherty (2005) collected infection data (N= 275 plots)—as described in Mathiasen and Hawksworth (1988)—for several conifers growing near western hemlocks severely infected with *Arceuthobium tsugense* subsp. *tsugense* across 24 study sites in Washington and Oregon.

From 2004–2006 Mathiasen and Daugherty (unpublished) determined the relative susceptibility of Pacific silver fir, noble fir, mountain hemlock, and western hemlock to *Arceuthobium tsugense* subsp. *amabilae*. They established temporary circular plots around large, severely infected trees (Pacific silver fir or noble fir) at five locations: Wildcat Mountain, Mary's Peak, Bunchgrass Mountain, Frissell Point, and Ollalie Ridge (Locations 3–7 on Fig. 3). In each plot, live trees taller than breast height were sampled and the species, DBH (nearest cm), and DMR were recorded. A total of 82 plots were established and 733 Pacific silver firs, 721 mountain hemlocks, 706 noble firs, and 268 western hemlocks were examined for infection by subsp. *amabilae*.

Mathiasen and Daugherty (2008) collected additional infection data for Pacific silver fir, noble fir, and mountain hemlock growing near trees severely infected (DMR 5 or 6) with subsp. *amabilae* (11 sites) or subsp. *mertensianae* (10 sites). A total of 215 plots were completed at the 21 sites. In each plot, live trees larger than five cm at DBH were sampled and the species, DBH (nearest cm), and DMR were recorded. At sites infested with subsp. *amabilae* 1397 Pacific silver firs, 1319 mountain hemlocks, and 772 noble firs were sampled; at sites infested with subsp. *mertensianae* 1506 mountain hemlocks, 145 noble firs, and 127 Pacific silver firs were sampled. No infection data for western white pine was collected by Mathiasen and Daugherty (2008); however, Mathiasen (2011) collected additional infection data for mountain hemlock and western white pine from three sites in northwestern California infested with subsp. *mertensianae*. Again, he used temporary six m radius, circular plots established around severely infected mountain hemlocks and recorded the species, DBH (nearest cm), and DMR for each live tree in a plot taller than breast height. A total of 30 plots were completed and 148 mountain hemlocks and 81 western white pines were sampled. Data from the above studies were combined and results summarized below.

## RESULTS

### Univariate Statistical Analyses

Results of the 1-way ANOVA by male and female morphologies indicated significant differences existed among *Arceuthobium campylopodum* and the four subspecies of *A. tsugense* (Table 1), while multiple comparisons of mean differences by female and male character also indicated significant differences among all taxa as well as separate morphological comparisons between each subspecies of *A. tsugense* to *A. campylopodum* (Table 2). Plants of *A. tsugense* subsp. *tsugense* and subsp. *amabilae* were the most similar among the subspecies, but they had several consistent morphological differences (Table 2). Male and female plants of subsp. *amabilae* were consistently larger than those of the other subspecies and the mean differences were significant. The mean heights of male and female plants of subsp. *mertensianae* and subsp. *contortae* were not significantly different. The mean basal diameters of male and female plants were significantly smaller than subsp. *amabilae* for subsp. *tsugense* and subsp. *mertensianae*. Although the mean basal diameter of male plants of subsp. *contortae* was only slightly smaller than that of subsp. *amabilae*, the difference was significant. The mean basal diameters of male and female plants were the smallest for subsp. *mertensianae*. The mean length of the third internode was

Table 1. One-way analysis of variance (ANOVA) testing by morphologic character for male and female plants of *Arceuthobium campylopodum* and *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae,* and *tsugense*.

| Character | Sum of Squares | | | Mean Square | | | |
|---|---|---|---|---|---|---|---|
| | Taxa | Error | Total | Taxa | Error | F-ratio | P-value |
| Plant height | | | | | | | |
| Female | 4270.0 | 8365.5 | 12635.5 | 1067.5 | 5.5 | $F_{4, 1510}$= 192.7 | <.0001 |
| Male | 3062.8 | 8734.5 | 11797.3 | 765.7 | 6.3 | $F_{4, 1385}$= 121.4 | <.0001 |
| Basal diameter | | | | | | | |
| Female | 250.7 | 722.7 | 973.4 | 62.7 | 0.5 | $F_{4, 1510}$= 131.0 | <.0001 |
| Male | 214.2 | 495.6 | 709.8 | 53.6 | 0.4 | $F_{4, 1385}$= 149.7 | <.0001 |
| Length of third internode | | | | | | | |
| Female | 3876.6 | 15356.0 | 19232.6 | 969.2 | 10.2 | $F_{4, 1510}$= 95.3 | <.0001 |
| Male | 2640.4 | 14237.4 | 16877.8 | 660.1 | 10.3 | $F_{4, 1385}$= 64.2 | <.0001 |
| Width of third internode | | | | | | | |
| Female | 239.9 | 176.7 | 416.5 | 60.0 | 0.1 | $F_{4, 1510}$= 512.5 | <.0001 |
| Female | 247.0 | 147.1 | 394.1 | 61.8 | 0.1 | $F_{4, 1385}$= 581.7 | <.0001 |
| Staminate spike length | 8298.5 | 27752.7 | 36051.2 | 2074.6 | 15.4 | $F_{4, 1805}$= 134.9 | <.0001 |
| Staminate spike width | 1407.2 | 374.9 | 1782.1 | 351.8 | 0.2 | $F_{4, 1805}$= 1694.0 | <.0001 |
| Flower diameter[a] | | | | | | | |
| 3-merous | 69.2 | 131.4 | 200.6 | 23.1 | 0.2 | $F_{3, 870}$ = 152.8 | <.0001 |
| 4-merous | 142.2 | 161.6 | 303.8 | 47.4 | 0.2 | $F_{3, 822}$ = 241.0 | <.0001 |
| 3- and 4-merous | 269.3 | 660.9 | 930.1 | 67.3 | 0.4 | $F_{4, 1805}$ = 184.0 | <.0001 |
| Petal length | 52.3 | 76.2 | 128.4 | 13.1 | 0.0 | $F_{4, 1805}$= 309.6 | <.0001 |
| Petal width | 38.9 | 58.9 | 97.8 | 9.7 | 0.0 | $F_{4, 1805}$= 298.5 | <.0001 |
| Anther diameter | 8.8 | 30.3 | 39.1 | 2.2 | 0.0 | $F_{4, 1805}$= 131.9 | <.0001 |
| Anther distance to tip | 28.3 | 47.5 | 75.8 | 7.1 | 0.0 | $F_{4, 1955}$= 291.3 | <.0001 |
| Fruit length | 370.3 | 258.8 | 629.1 | 92.6 | 0.2 | $F_{4, 1205}$= 431.1 | <.0001 |
| Fruit width | 188.0 | 147.5 | 335.4 | 47.0 | 0.1 | $F_{4, 1205}$= 384.0 | <.0001 |
| Seed length | 156.5 | 143.9 | 300.4 | 39.1 | 0.1 | $F_{4,1185}$= 322.3 | <.0001 |
| Seed width | 34.0 | 26.1 | 60.1 | 8.5 | 0.0 | $F_{4, 1185}$= 386.2 | <.0001 |

significantly different among the subspecies except for female plants of subsp. *mertensianae* and subsp. *contortae* (Table 2). In addition, the color of female plants of subsp. *amabilae* were frequently green or green-brown, while the color of female plants of subsp. *tsugense* were consistently yellow-green or purple (Hawksworth & Wiens 1996; Mathiasen & Daugherty 2007). Male plants of subsp. *tsugense* were typically yellow-green, while the male plants of the other subspecies were more often green-brown, but some male plants of each subspecies were yellow-green.

The mean lengths and widths of staminate spikes were significantly different among the subspecies (Table 2). The mean length and width of the staminate spikes of subsp. *mertensianae* were the smallest of all the subspecies. Staminate flowers of subsp. *amabilae* were similar in size to those of subsp. *tsugense*, but both of these subspecies have flowers that were consistently larger than the flowers of subsp. *mertensianae* (Table 2). Although Hawksworth et al. (1992) and Hawksworth and Wiens (1996) reported that staminate flower diameters of subsp. *mertensianae* were similar to those of subsp. *tsugense*, our measurements indicated that the staminate flowers of subsp. *mertensianae* were consistently smaller than those of all the other subspecies. The mean length and width of petals were significantly different across the subspecies. An important characteristic of subsp. *contortae* was that male flowers had the longest petals on average of any of the taxa examined and, hence, had the largest mean flower diameters when considering 3- and 4-merous flowers combined (Table 2). Shore pine dwarf mistletoe also had anthers that were on average the furthest from the tip of petals. The mean diameter of anthers was similar for the taxa studied except for subsp. *mertensianae* which had significantly smaller anthers.

The mean length of fruits of *Arceuthobium tsugense* subsp. *contortae* was not significantly different than subsp. *tsugense* and subsp. *amabilae*, but fruits of subsp. *mertensianae* were significantly smaller when compared to the other three subspecies (Table 2). The mean width of fruits followed a similar pattern; fruits of

Table 2. Morphological comparison of male and female plants for *Arceuthobium campylopodum*, *A. tsugense* subsp. *amabilae*, *A. tsugense* subsp. *contortae*, *A. tsugense* subsp. *mertensianae*, and *A. tsugense* subsp. *tsugense*. Data are listed as mean (95% confidence interval, α= 0.05) [N= measurements]. Lower case letters in brackets designate measurement sizes already listed in the same column. Means followed by different capital letters in the same row were significantly different according to a Tukey's honestly significant difference (HSD) test (α= 0.05). Likewise, by row, bolded cells indicate a significant difference in mean measurement compared to *A. campylopodum* (control) using a Dunnett's test. Plant heights are in cm whereas all other measurements are in mm. a—Plant height (PH), basal diameter (BD), length and width of third internode (LTI, WTI), staminate spike length and width (SSL, SSW), flower diameter (FD), petal length and width (PL, PW), anther diameter (AD), anther distance to tip (ADT), fruit length and width (FL, FW), and seed length and width (SL, SW). Measurements of FD for subsp. *contortae* did not distinguish between 3- and 4-merous flowers so comparisons were made with the other taxa by combining all FD measurements.

| | *Arceuthobium* | | | | |
|---|---|---|---|---|---|
| **Character** | *campylopodum* | *amabilae* | *contortae* | *mertensianae* | *tsugense* |
| **PH** | | | | | |
| Female | 10.4 A (±0.2) [600a] | 10.6 A (±0.2) [380a] | **6.6 B (±0.2) [110a]** | **6.1 B (±0.3) [160a]** | **8.0 C (±0.2) [265a]** |
| Male | 9.7 A (±0.2) [a] | 9.4 A (±0.3) [280b] | **5.6 B (±0.3) [a]** | **5.7 B (±0.3) [130b]** | **7.8 C (±0.5) [270b]** |
| **BD** | | | | | |
| Female | 3.4 A (±0.1) [a] | 3.4 A (±0.1) [388] | 3.3 A (±0.1) [a] | **2.2 B (±0.1) [a]** | **2.7 B (±0.1) [a]** |
| Male | 3.2 A (±0.0) [a] | **3.1 B (±0.1) [b]** | **2.8 C (±0.1) [a]** | **1.9 D (±0.1) [b]** | **2.6 E (±0.1) [b]** |
| **LTI** | | | | | |
| Female | 13.0 A (±0.2) [a] | **15.0 B (±0.4) [a]** | **10.7 C (±0.4) [a]** | **9.8 C (±0.5) [a]** | **12.3 D (±0.4) [a]** |
| Male | 11.9 A (±0.3) [a] | **12.6 B (±0.4) [b]** | **9.2 C (±0.4) [a]** | **8.0 D (±0.6) [b]** | 11.8 A (±0.4) [b] |
| **WTI** | | | | | |
| Female | 2.5 A (±0.0) [a] | **2.0 B (±0.0) [a]** | **1.7 C (±0.0) [a]** | **1.4 D (±0.0) [a]** | **1.6 C (±0.1) [a]** |
| Male | 2.5 A (±0.0) [a] | **1.9 B (±0.0) [b]** | **1.8 B (±0.0) [a]** | **1.3 C (±0.0) [b]** | **1.6 D (±0.0) [b]** |
| SSL | 12.7 A (±0.3)[760b] | **9.5 B (±0.4) [a]** | 12.6 A (±0.6) [a] | **6.9 C (±0.2) [300c]** | **10.8 D (±0.4) [260c]** |
| SSW | 3.0 A (±0.0) [b] | **1.3 B (±0.0) [a]** | **3.4 C (±0.1) [a]** | **1.2 D (±0.0) [c]** | **1.6 E (±0.1) [c]** |
| **FD** | | | | | |
| 3-merous | 3.1 A (±0.1) [400] | **3.2 A (±0.1) [210]** | — | **2.4 B (±0.0) [150d]** | 3.1 A (±0.1) [115d] |
| 4-merous | 4.2 A (±0.0) [360] | **3.7 B (±0.1) [200]** | — | **3.1 C (±0.0) [d]** | **3.8 B (±0.1) [d]** |
| 3&4-merous | 3.6 A (±0.0) [b] | **3.4 B (±0.1) [410]** | **4.3 C (±0.1) [a]** | **2.7 D (±0.0) [c]** | **3.5 B (±0.1) [230]** |
| PL | 1.6 A (±0.0) [b] | **1.4 B (±0.0) [a]** | **1.7 A (±0.1) [a]** | **1.1 C (±0.0) [c]** | **1.5 D (±0.0) [c]** |
| PW | 1.4 A (±0.0) [b] | **1.2 B (±0.0) [a]** | 1.4 A (±0.0) [a] | **1.0 C (±0.0) [c]** | **1.2 B (±0.0) [c]** |
| AD | 0.6 A (±0.0) [b] | **0.7 B (±0.0) [a]** | **0.7 B (±0.0) [a]** | **0.5 C (±0.0) [c]** | **0.7 B (±0.0) [c]** |
| ADT | 0.6 A (±0.0) [910] | **0.5 B (±0.0) [a]** | **0.9 C (±0.0) [a]** | **0.4 D (±0.0) [c]** | **0.5 E (±0.0) [c]** |
| FL | 5.4 A (±0.0) [480c] | **4.7 B (±0.1) [260b]** | **4.6 BD (±0.1) [a]** | **3.8 C (±0.1) [d]** | **4.4 D (±0.0) [210f]** |
| FW | 3.7 A (±0.0) [c] | **3.0 B (±0.0) [b]** | **3.1 B (±0.1) [a]** | **2.6 C (±0.1) [d]** | **2.9 D (±0.0) [e]** |
| SL | 3.5 A (±0.0) [c] | **3.0 B (±0.0) [b]** | **2.5 C (±0.1)[100b]** | **2.8 D (±0.0) [d]** | **2.6 E (±0.0) [200f]** |
| SW | 1.5 A (±0.0) [c] | **1.2 B (±0.0) [b]** | **1.4 C (±0.0) [b]** | **1.1 D (±0.0) [d]** | **1.1 B (±0.0) [f]** |

subsp. *mertensianae* were the narrowest on average, whereas, the mean length of seeds was significantly different between all of the subspecies. The mean width of seeds for subsp. *tsugense* and subsp. *mertensianae* was significantly smaller than subsp. *amabilae* and subsp. *contortae*.

Morphologically, *Arceuthobium campylopodum* was most similar to *A. tsugense* subsp. *amabilae*, but differed significantly when compared to subsp. *amabilae* across four of eight (4/8) and 11 out of 12 (11/12) female and male characters, respectively, including mean basal diameter, third internode length and width, staminate spike length and width, 4-merous male flower diameter, petal dimensions, and anther diameter and distance to tip (Tables 1 and 2). Mean fruit and seed dimensions of *A. campylopodum* were also significantly greater than those of subsp. *amabilae*. *Arceuthobium campylopodum* was morphologically quite distinct from *A. tsugense* subsp. *contortae*, subsp. *mertensianae*, and subsp. *tsugense*. No statistical mean differences were found between *A. campylopodum* and subsp. *contortae* when comparing basal diameter of female plants as well as staminate spike length and petal width; however, of the remaining seven female (7/8) and ten male (10/12) characters, all were significantly different between these two taxa. Likewise, for *A. campylopodum* versus subsp. *contortae*, all mean differences by female character were significant; whereas, the means for 10 of 12 male plant parts were also significantly different with *A. campylopodum* and subsp. *contortae* sharing morphological similarity in only third internode length of male plants. Moreover, mean differences between *A. campylopodum* and *A. tsugense* subsp. *mertensianae* across all female (8/8) and male (12/12) characters were significant, with *A.*

*campylopodum* consistently producing larger female and male plants as well as unlike fruit, seed, and staminate flower morphologies when compared directly to subsp. *mertensianae*.

### Multivariate Statistical Analyses

Multivariate analysis of variance (MANOVA) by plant sex indicated that there were significant differences among the 8 female (Wilks' Lambda approx. $F_{32,\,4346}$= 147.8, *P*< 0.0001; Pilllai's Trace approx. $F_{32,\,4724}$= 105.9, *P*< 0.0001; Hotelling-Lawley approx. $F_{32,\,3070}$= *P*< 0.0001) and 10 male morphological characters (Wilks' Lambda approx. $F_{40,\,5181.16}$= 144.2, *P*< 0.0001; Pilllai's Trace approx. $F_{40,\,5476}$= 99.2, *P*< 0.0001; Hotelling-Lawley approx. $F_{40,\,3812.6}$= 201.8, *P*< 0.0001) among the four subspecies of *Arceuthobium tsugense* and *A. campylopodum*. Separately analyzing these same 8 female and 10 male characteristics (full-model), standard DFA correctly classified a total of 86.6% (1031/1190) and 83.9% (1158/1380) of female and male plants diagnosed in the field to the correct taxon, respectively (Table 3). Means with associated 95% confidence intervals for female and male characteristics by predicted taxon according to standard DFA (full-model with equal prior probabilities per taxon) of complete morphological records are presented in Table 4. The first two discriminant functions (canonicals) explained a total of 90.8% of the variation among the complete records of female (N= 1190) and male plants (N= 1380) of *A. campylopodum* and the four subsp. of *A. tsugense* (Table 5). Inspection of the standard DFA for female plants revealed that *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae*, and *tsugense* were classified correctly 82.3%, 98%, 86.7%, and 68.5% on the time, respectively. The multivariate mean of female plants among all four subspecies did not intersect in multidimensional space in the standard DFA utilizing complete or resampled data (Fig. 5A and C); however, the distribution of multivariate means for female *A. tsugense* subsp. *tsugense* was considerable—overlapping with subsp. *amabilae* and *mertensianae* and, to a lesser extent, subsp. *contortae*. As a consequence, female plants of the latter taxon—*A. tsugense* subsp. *tsugense*—were most frequently misclassified using standard DFA and complete records to subsp. *mertensianae* (12.5%) followed by subsp. *amabilae* (9.0%) and subsp. *contortae* (6.0%; Table 5). However, it is important to note that subsp. *tsugense* was rarely classified as *A. campylopodum* (3.5%) when considering all female characters and complete data (Table 6). Likewise, female *A. tsugense* subsp. *amabilae* were rarely assigned to subsp. *contortae* (0.4%), subsp. *mertensianae* (3.1%), and *A. campylopodum* (2.3%) as well as only occasionally placed to subsp. *tsugense* (8.1%). Female plants of *A. tsugense* subsp. *mertensianae* were also occasionally predicted to subsp. *tsugense* (8.7%) and rarely classified to either subsp. *amabilae* (4.0%) or subsp. *contortae* (0.7%). None of the complete female records for *A. tsugense* subsp. *mertensianae* were classified to *A. campylopodum* according to standard DFA and, using the same statistical approach, subsp. *contortae* was predicted to *A. campylopodum* only 1% of the time (Table 6). Standard DFA also clearly delimited female *A. tsugense* subsp. *contortae* from female plants of subsp. *amabilae* (0.0%), subsp. *mertensianae* (0.0%), and subsp. *tsugense* (1%). Moreover, of the 480 female plants of *A. campylopodum* included in the standard DFA, only 28 were misclassified to one of three subspecies of *A. tsugense*: *amabilae* (4.4%, 21/480), *contortae* (0.8%, 4/480), and *tsugense* (0.6%, 3/480; Table 5). Consequently, female plants determined a priori to *A. campylopodum* were not classified to *A. tsugense* subsp. *mertensianae* (0.0%, 0/452) and only rarely to subsp. *amabilae*, *contortae*, and *tsugense* using standard DFA.

The characteristics contributing most to the prediction of female plants to taxon membership using full-model DFA were fruit length, third internode width, and seed dimensions (Table 7). In fact, integrating the four aforementioned female plant morphologies alone in the DFA resulted in an overall correct classification of 80.2% across taxa, including ≥84% of female plants for *A. tsugense* subsp. *contortae* (90%) and subsp. *mertensianae* (84%) as well as *A. campylopodum* (90.6%; Table 3). The sequential addition of six female characters to include basal diameter and plant height increased the discriminatory power of the DFA model; correctly predicting 84.7% of taxa while assigning >80% of *A. tsugense* subsp. *amabilae* (80.8%), *contortae* (97%), and *mertensianae* (86.7%) to the correct taxonomic membership. As with the standard DFA for female plants, results for the stepwise DFA indicated that *A. tsugense* subsp. *tsugense* was often misclassified to one of the three other subspecies; yet, subsp. *tsugense* was rarely assigned to *A. campylopodum*. Moreover, *A. tsugense* subsp. *tsugense* was classified correctly >59% of the time utilizing only fruit length in the discriminant function (Table 3).

Table 3. Forward, stepwise discriminant function analysis (DFA): classification of female and male plants of *Arceuthobium campylopodum* and subspecies of *A. tsugense* to species membership via sequential addition of morphological characters most correlated to the discriminant function. a—Plant height (PH), basal diameter (BD), length and width of third internode (LTI, WTI), staminate spike length and width (SSL, SSW), flower diameter (FD), petal length and width (PL, PW), anther diameter (AD), anther distance to tip (ADT), fruit length and width (FL, FW), and seed length and width (SL, SW).

| | **Correct species membership (%, [N predicted/ N field determined])** | | | | | |
|---|---|---|---|---|---|---|
| | | | ***Arceuthobium tsugense* subsp.** | | | |
| **Stepwise DFA (step [character])** | **Total** | ***A. campylopodum*** | ***amabilae*** | ***contortae*** | ***mertensianae*** | ***tsugense*** |
| **Female** | | | | | | |
| 1. [FL] | 56.0 [666/1190] | 77.5 [372/480] | 19.2 [50/260] | 7.0 [7/100] | 78.7 [118/150] | 59.5 [119/200] |
| 2 [*], [WTI] | 64.9 [772/1190] | 82.9 [398/480] | 45.0 [117/260] | 62.0 [62/100] | 76.0 [114/150] | 40.5 [81/200] |
| 3 [*], [*], [SL] | 75.3 [896/1190] | 87.5 [420/480] | 71.5 [186/260] | 78.0 [78/100] | 84.0 [126/150] | 43.0 [86/200] |
| 4 [*], [*], [*], [SW] | 80.2 [954/1190] | 90.6 [435/480] | 77.3 [201/260] | 90.0 [90/100] | 84.0 [126/150] | 51.0 [102/200] |
| 5 [*], [*], [*], [*], [BD] | 81.9 [975/1190] | 92.3 [443/480] | 79.2 [206/260] | 93.0 [93/100] | 85.3 [128/150] | 52.5 [105/200] |
| 6 [*], [*], [*], [*], [*],[PH] | 84.7 [1008/1190] | 92.9 [446/480] | 80.8 [210/260] | 97.0 [97/100] | 86.7 [130/150] | 62.5 [125/200] |
| 7 [*], [*], [*], [*], [*],[*], [LTI] | 85.8 [1021/1190] | 93.5 [449/480] | 81.9 [213/260] | 98.0 [98/100] | 85.3 [128/150] | 66.5 [133/200] |
| 8 [*], [*], [*], [*], [*],[*], [*], [FW] | 86.6 [1031/1190] | 94.2 [452/480] | 82.3 [214/260] | 98.0 [98/100] | 86.7 [130/150] | 68.5 [137/200] |
| **Male** | | | | | | |
| 1 [SSW] | 60.9 [841/1380] | 84.5 [507/600] | 67.5 [189/280] | 41.8 [46/110] | 70.0 [91/130] | 3.1 [8/260] |
| 2 [*], [LTI] | 71.2 [983/1380] | 88.0 [528/600] | 78.6 [220/280] | 91.8 [101/110] | 93.1 [121/130] | 3.1 [8/260] |
| 3 [*, [*], [AD] | 73.1 [1009/1380] | 87.5 [525/600] | 85.7 [240/280] | 89.1 [98/110] | 96.9 [126/130] | 7.7 [20/260] |
| 4 [*], [*], [*], [ADT] | 76.4 [1054/1380] | 93.3 [560/600] | 86.1[241/280] | 89.1 [98/110] | 96.9 [126/130] | 11.2 [29/260] |
| 5 [*], [*], [*], [*], [BD] | 77.5 [1070/1380] | 93.5 [561/600] | 88.9 [249/280] | 90.0 [99/110] | 96.9 [126/130] | 13.5 [35/260] |
| 6 [*], [*], [*], [*], [*], [LTI] | 79.3 [1094/1380] | 93.3 [560/600] | 90.0 [252/280] | 88.2 [97/110] | 96.9 [126/130] | 15.0 [39/260] |
| 7 [*], [*], [*], [*], [*], [*], [PH] | 80.4 [1109/1380] | 92.7 [556/600] | 88.9 [249/280] | 90.9 [100/110] | 97.7 [127/130] | 29.6 [77/260] |
| 8 [*], [*], [*], [*], [*], [*], [*], [PL] | 81.8 [1129/1380] | 92.7 [556/600] | 89.3 [250/280] | 93.6 [103/110] | 98.5 [128/130] | 35.4 [92/260] |
| 9 [*], [*], [*], [*], [*], [*], [*], [*], [SSL] | 83.7 [1155/1380] | 94.0 [564/600] | 90.7 [254/280] | 91.8 [101/110] | 98.5 [128/130] | 41.5 [108/260] |
| 10 [*], [*], [*], [*], [*], [*], [*], [*], [*], [PW] | 83.9 [1158/1380] | 93.7 [562/600] | 90.7 [254/280] | 92.7 [102/110] | 97.7 [127/130] | 43.5 [113/260] |

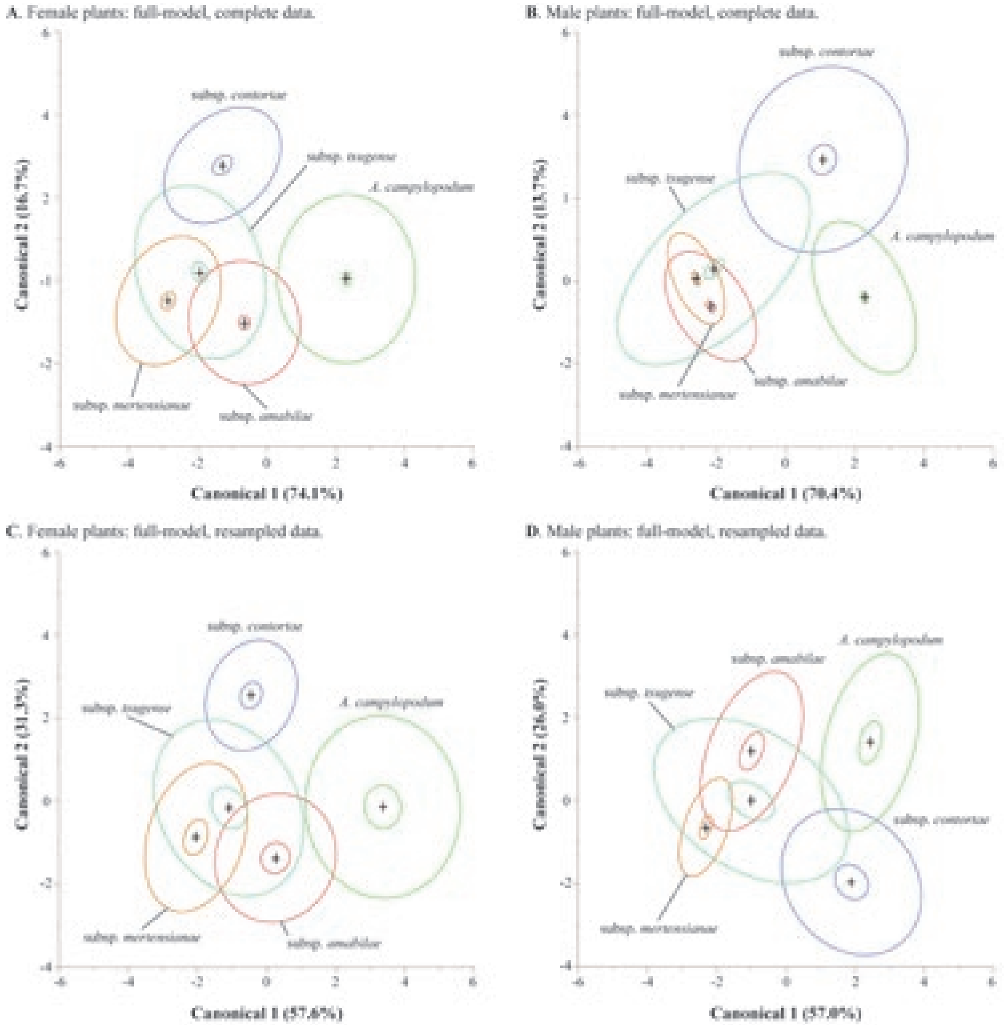
Table 4. Full-model, quadratic discriminant function analysis for female and male plants. Means and 95% confidence intervals for morphological characters according to predicted species membership. Plant height is in cm whereas all other mean measurements by character are in mm.

| | | ***Arceuthobium tsugense*** **subsp.** | | | |
|---|---|---|---|---|---|
| **Sex / Character(s)** | *A. campylopodum* | *amabilae* | *contortae* | *mertensianae* | *tsugense* |
| **Female** | | | | | |
| Plant height (PH) | 10.3 (±0.2) | 11.0 (±0.3) | 6.6 (±0.2) | 6.0 (±0.3) | 8.1 (±0.3) |
| Basal diameter (BA) | 3.4 (±0.1) | 3.5 (±0.1) | 3.3 (±0.1) | 2.1 (±0.1) | 2.6 (±0.1) |
| Length of third internode (LTI) | 13.0 (±0.3) | 15.5 (±0.5) | 10.7 (±0.4) | 9.7 (±0.4) | 12.7 (±0.5) |
| Width of third internode (WTI) | 2.5 (±0.0) | 2.1 (±0.0) | 1.7 (±0.0) | 1.3 (±0.0) | 1.6 (±0.1) |
| Fruit length (FL) | 5.4 (±0.0) | 4.7 (±0.1) | 4.6 (±0.1) | 3.8 (±0.1) | 4.5 (±0.0) |
| Fruit width (FW) | 3.7 (±0.0) | 3.1 (±0.0) | 3.1 (±0.1) | 2.6 (±0.1) | 3.0 (±0.0) |
| Seed length (SL) | 3.5 (±0.0) | 3.1 (±0.0) | 2.5 (±0.0) | 2.8 (±0.0) | 2.6 (±0.0) |
| Seed width (SW) | 1.5 (±0.0) | 1.2 (±0.0) | 1.4 (±0.0) | 1.1 (±0.0) | 1.1 (±0.0) |
| **Male** | | | | | |
| Plant height (PH) | 9.8 (±0.2) | 9.2 (±0.2) | 5.9 (±0.2) | 6.0 (±0.2) | 8.0 (±0.4) |
| Basal diameter (BA) | 3.2 (±0.1) | 3.0 (±0.1) | 2.8 (±0.1) | 2.0 (±0.1) | 2.6 (±0.1) |
| Length of third internode (LTI) | 12.0 (±0.3) | 12.6 (±0.3) | 9.3 (±0.3) | 8.6 (±0.5) | 12.1 (±0.6) |
| Width of third internode (WTI) | 2.5 (±0.0) | 1.8 (±0.0) | 1.8 (±0.0) | 1.3 (±0.0) | 1.6 (±0.1) |
| Petal length (PL) | 1.5 (±0.0) | 1.4 (±0.0) | 1.7 (±0.1) | 1.1 (±0.0) | 1.5 (±0.0) |
| Petal width (PW) | 1.4 (±0.0) | 1.3 (±0.0) | 1.4 (±0.0) | 1.0 (±0.0) | 1.2 (±0.0) |
| Anther diameter (AD) | 0.6 (±0.0) | 0.7 (±0.0) | 0.7 (±0.0) | 0.5 (±0.0) | 0.7 (±0.0) |
| Anther distance from tip (ADT) | 0.6 (±0.0) | 0.5 (±0.0) | 0.9 (±0.0) | 0.4 (±0.0) | 0.6 (±0.0) |
| Staminate spike length (SSL) | 13.0 (±0.4) | 10.2 (±0.4) | 12.3 (±0.5) | 6.9 (±0.3) | 11.6 (±0.7) |
| Staminate spike width (SSW) | 3.0 (±0.0) | 1.3 (±0.0) | 3.4 (±0.1) | 1.1 (±0.0) | 2.0 (±0.2) |

Table 5. Canonical statistics: standard discriminant function analyses (DFA) of female and male plants of *Arceuthobium campylopodum and A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae,* and *tsugense.* DFAs were executed using a full-model (N= 8 female or 10 male characters) and equal prior probabilities (0.2). Canonical details by plant sex are subdivided according to analyses performed on the complete and randomized resampled (50 complete records/species) datasets.

| **Canonical** | **Eigenvalue** | **Percentage** | **Cumulative percentage** | **Canonical correlation** | **Likelihood Ratio** | **Approximant F** | ***P*-value** |
|---|---|---|---|---|---|---|---|
| **Female - Complete** | | | | | | | |
| 1 | 4.07 | 74.10 | 74.10 | 0.8959 | 0.0662 | $F_{32, 4345.8}$= 147.75 | <.0001 |
| 2 | 0.92 | 16.70 | 90.81 | 0.6916 | 0.3355 | $F_{21, 3386}$= 74.63 | <.0001 |
| 3 | 0.37 | 6.66 | 97.47 | 0.5174 | 0.6430 | $F_{12, 2360}$= 48.60 | <.0001 |
| 4 | 0.14 | 2.53 | 100.00 | 0.3493 | 0.8780 | $F_{5, 1181}$= 32.82 | <.0001 |
| **Female - Resampled** | | | | | | | |
| 1 | 3.45 | 57.57 | 57.57 | 0.8805 | 0.0448 | $F_{32, 879.3}$= 36.30 | <.0001 |
| 2 | 1.87 | 31.30 | 88.87 | 0.8075 | 0.1993 | $F_{21, 686.8}$= 24.65 | <.0001 |
| 3 | 0.51 | 8.58 | 97.45 | 0.5827 | 0.5730 | $F_{12, 480}$= 12.84 | <.0001 |
| 4 | 0.15 | 2.55 | 100.00 | 0.3639 | 0.8676 | $F_{5, 241}$= 7.36 | <.0001 |
| **Male—Complete** | | | | | | | |
| 1 | 4.78 | 77.12 | 77.12 | 0.9093 | 0.0586 | $F_{40, 5181.6}$= 144.24 | <.0001 |
| 2 | 0.85 | 13.67 | 90.80 | 0.6771 | 0.3382 | $F_{27, 3993}$= 66.47 | <.0001 |
| 3 | 0.51 | 8.21 | 99.01 | 0.5805 | 0.6246 | $F_{16, 2736}$= 45.37 | <.0001 |
| 4 | 0.06 | 0.99 | 100.00 | 0.2407 | 0.9421 | $F_{7, 1369}$= 12.03 | <.0001 |
| **Male - Resampled** | | | | | | | |
| 1 | 3.43 | 56.97 | 56.97 | 0.8799 | 0.0411 | $F_{40, 896.7}$= 29.59 | <.0001 |
| 2 | 1.56 | 25.94 | 82.91 | 0.7807 | 0.1822 | $F_{27, 692.8}$= 20.31 | <.0001 |
| 3 | 0.90 | 14.95 | 97.86 | 0.6881 | 0.4664 | $F_{16, 476}$= 13.81 | <.0001 |
| 4 | 0.13 | 2.14 | 100.00 | 0.3379 | 0.8858 | $F_{7, 239}$= 4.40 | 0.0001 |

However, despite the stepwise addition of female characters into the DFA model—such as third internode length, seed length and width, and basal diameter—the overall accuracy of the model for classifying correctly field determined female plants of subsp. *tsugense* decreased. This result was consistent with the univariate


A. Female plants: full-model, complete data.

B. Male plants: full-model, complete data.

C. Female plants: full-model, resampled data.

D. Male plants: full-model, resampled data.

**Fig. 5. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. tsugense* subsp. *tsugense*, subsp. *amabilae*, subsp. *contortae*, and subsp. *mertensianae* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 3. Multivariate means (cross hairs) were computed using complete data for each species by sex (A, B) or a random subset (50 complete records/species) of female (C) and male plants (D), respectively. The inner ellipses correspond to a 95% confidence limit for the mean, and the outer ellipses represent a normal 50% contour wherein 50% of plants for each taxon reside.**

comparisons of fruit length, female third internode and seed widths, and female basal diameter among the four subspecies, where the individual means for subsp. *tsugense* across these female characters were not statistically different when compared to subsp. *amabilae*, *contortae*, and/or *mertensianae* (Table 2).

As with DFA for female plants, standard DFA of male morphology utilizing complete data and equal prior probabilities across taxa resulted in the consistent classification *Arceuthobium tsugense* subsp. *amabilae* (90.7%), *contortae* (92.7%), and *mertensianae* (97.7%) to correct taxonomic membership as well as the clear separation of all four subspecies when compared to *A. campylopodum* (Table 6; Fig. 5). However, unlike the female DFAs, >50% of male *A. tsugense* subsp. *tsugense* were misclassified when considering simultaneously all 10 male characters in the model. Subspecies *tsugense* was regularly misclassified to subsp. *amabilae* 38.1% of

Table 6. Standard discriminant function (DFA): assignment of field determined female and male plants of *Arceuthobium campylopodum* and *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae*, and *tsugense* utilizing 8 female and 10 male characters (full-model per sex) as well as equal prior probability per taxon (0.2).

| | **Assigned species membership (%, [N= field determined plants]) according to DFA** | | | | |
|---|---|---|---|---|---|
| | | ***Arceuthobium tsugense*** **subsp.** | | | |
| **Plant sex / *Arceuthobium* taxon (Total N = field determined plants)** | ***A. campylopodum*** | ***amabilae*** | ***contortae*** | ***mertensianae*** | ***tsugense*** |
| **Female** | | | | | |
| *A. campylopodum* (480) | 94.2 [452] | 4.4 [21] | 0.8 [4] | 0.0 [0] | 0.6 [3] |
| *A. tsugense* subsp. *amabilae* (260) | 2.3 [6] | 82.3 [214] | 0.4 [1] | 3.1 [8] | 8.1 [21] |
| *A. tsugense* subsp. *contortae* (100) | 1.0 [1] | 0.0 [0] | 98.0 [98] | 0.0 [0] | 1.0 [1] |
| *A. tsugense* subsp. *mertensianae* (150) | 0.0 [0] | 4.0 [6] | 0.7 [1] | 86.7 [130] | 8.7 [13] |
| *A. tsugense* subsp. *tsugense* (200) | 3.5 [7] | 9.5 [19] | 6.0 [12] | 12.5 [25] | 68.5 [137] |
| **Male** | | | | | |
| *A. campylopodum* (600) | 93.7 [562] | 0.0 [0] | 5.2 [31] | 0.0 [0] | 1.2 [7] |
| *A. tsugense* subsp. *amabilae* (280) | 0.0 [0] | 90.7 [254] | 0.7 [2] | 5.0 [14] | 3.6 [10] |
| *A. tsugense* subsp. *contortae* (110) | 3.6 [4] | 0.0 [0] | 92.7 [102] | 0.0 [0] | 3.6 [4] |
| *A. tsugense* subsp. *mertensianae* (130) | 0.0 [0] | 0.8 [1] | 0.0 [0] | 97.7 [127] | 1.5 [2] |
| *A. tsugense* subsp. *tsugense* (260) | 1.2 [3] | 38.1 [99] | 4.6 [12] | 12.7 [33] | 43.5 [113] |

Table 7. Standard discriminant function analysis (DFA) of female and male morphologies (N= 8 and 10 male characters, respectively) of *Arceuthobium campylopodum* and *A. tsugense* subsp. *amabilae*, *contortae*, *mertensianae,* and *tsugense*: standardized correlation coefficients by canonical (Can.), indicating the individual contribution of each morphologic character to the classification of species membership. a—Plant height (PH), basal diameter (BD), length and width of third internode (LTI, WTI), staminate spike length and width (SSL, SSW), flower diameter (FD), petal length and width (PL, PW), anther diameter (AD), anther distance to tip (ADT), fruit length and width (FL, FW), and seed length and width (SL, SW).

| | **Female** | | | | **Male** | | | |
|---|---|---|---|---|---|---|---|---|
| **Character** | **Can. 1** | **Can. 2** | **Can. 3** | **Can. 4** | **Can. 1** | **Can. 2** | **Can. 3** | **Can. 4** |
| PH | 0.23 | -0.50 | 0.10 | -0.27 | 0.00 | -0.54 | -0.04 | -0.03 |
| BD | -0.23 | 0.37 | 0.81 | 0.94 | -0.16 | 0.26 | 0.50 | -0.67 |
| LTI | -0.30 | -0.08 | 0.40 | -0.39 | -0.24 | 0.23 | 0.26 | 0.87 |
| WTI | 0.76 | -0.16 | -0.45 | -0.09 | 0.74 | -0.52 | -0.03 | -0.19 |
| FL | 0.36 | 0.02 | 0.39 | -0.34 | | | | |
| FW | 0.18 | 0.21 | -0.06 | -0.25 | | | | |
| SL | 0.26 | -0.93 | -0.28 | 0.50 | | | | |
| SW | 0.29 | 0.85 | -0.15 | 0.04 | | | | |
| PL | | | | | -0.05 | 0.21 | 0.42 | 0.48 |
| PW | | | | | 0.12 | -0.19 | -0.05 | -0.11 |
| AD | | | | | -0.30 | -0.12 | 0.46 | -0.27 |
| ADT | | | | | -0.24 | 0.59 | 0.25 | -0.39 |
| SSL | | | | | -0.02 | -0.13 | 0.11 | 0.41 |
| SSW | | | | | 0.90 | 0.28 | -0.30 | 0.18 |

the time followed by subsp. *mertensianae* (12.7%) and, rarely, subsp. *contortae* (4.6%; Table 5). In conjunction, staminate spike width, third internode length, and anther diameter provided the most discriminatory power among male plants of subsp. *amabilae*, *contortae*, and *mertensianae* as well as *A. campylopodum* (Table 7). Utilizing complete data for these three male characters alone within the DFA model correctly assigned 73.1% of all male plants to their corresponding taxonomic membership, including high accuracy for *A. campylopodum* (87.5%) and *A. tsugense* subsp. *amabilae* (85.7%), *contortae* (89.1%), and *mertensianae* (96.9%; Table 3). The sequential addition of male characters to the DFA model further improved the frequency of correct classification of all taxa besides *A. tsugense* subsp. *tsugense*. Like female plants of *A. tsugense* subsp. *tsugense*, the morphological variation among individual male plants classified to subsp. *tsugense* was remarkably greater when compared to subsp. *amabilae* and *mertensianae* (Table 5), while the individual multivariate means for these three subspecies were closely associated in multidimensional space utilizing either complete or resampled data (Fig. 5B and D). Although often and occasionally misclassified to subsp. *amabilae* and *mertensianae*, male plants of *A. tsugense* subsp. *tsugense* were readily distinguished from subsp. *contortae* and *A. campylopodum* with the full-model DFA utilizing complete or resampled data.

### Host Susceptibility Based on Natural Infection

Host susceptibility data based on natural infection of conifers by the subspecies of *Arceuthobium tsugense* from the studies listed above were summarized in Table 8. Nearly 2500 western hemlocks were sampled in three studies and 96% of the trees were infected by *A. tsugense* subsp. *tsugense* which demonstrated that western hemlock is the principal host of this subspecies (Mathiasen & Hawksworth 1988; Wass & Mathiasen 2003; Mathiasen & Daugherty 2005). In addition, the mean DMR for the sampled western hemlocks was 3.1 which indicated that many of the sampled trees were severely infected. Because Pacific silver fir, mountain hemlock, and noble fir were infected at much lower levels than western hemlock and with infection incidences of 35%, 27%, and 14%, respectively, these conifers were classified as occasional hosts of subsp. *tsugense* (Table 8). Although the sample size was relatively small for shore pine infected by subsp. *tsugense* on Vancouver Island, B.C. (77 trees), only 1% of the shore pines sampled were infected which indicated shore pine should be classified as a rare host of subsp. *tsugense* (Wass & Mathiasen 2003). Thus far, two studies have sampled over 400 western white pines growing near western hemlocks severely infected with subsp. *tsugense* and no infected trees were observed (Mathiasen & Hawksworth 1988; Mathiasen & Daugherty 2005). However, rare infection of western white pine by subsp. *tsugense* has been reported (Gill 1935; Hunt & Smith 1978).

Ninety-seven percent (97%) of the shore pine sampled (1576 trees) in the plots located in dwarf mistletoe-infested shore pine forests were infected by *Arceuthobium tsugense* subsp. *contortae* and these trees had a mean DMR of 4.3 (Table 8) (Wass & Mathiasen 2003). Of the 802 western hemlocks sampled in these forests, only 21% were infected by subsp. *contortae*; these western hemlocks only had a mean DMR of 0.3. These infection levels (% infection) indicated that shore pine was a principal host of subsp. *contortae* and western hemlock was an occasional host.

Pacific silver fir, noble fir, and mountain hemlock were all highly susceptible to infection (> 90% trees infected) by *Arceuthobium tsugense* subsp. *amabilae* and were classified as principal hosts of this mistletoe (Table 8). In contrast, only 18% of the 268 western hemlocks growing near severely infected Pacific silver firs or noble firs were infected and their mean DMR was 0.4. The low mean DMR for western hemlock contrasts dramatically with the much greater mean DMRs for Pacific silver fir (3.6), noble fir (2.9), or mountain hemlock (3.1) from the same locations. Observations at other locations in southern Oregon support the classification of western hemlock as an occasional host of subsp. *amabilae* (Mathiasen & Daugherty unpublished). Mathiasen and Daugherty (2008) also reported that Pacific silver fir, noble fir, and mountain hemlock were principal hosts of subsp. *amabilae*. They sampled 1397 additional Pacific silver firs, 1248 mountain hemlocks, and 772 noble firs growing near large Pacific silver or noble firs severely infected by subsp. *amabilae* and reported infection percentages of 95%, 90%, and 93%, respectively. These data are combined with data collected by Mathiasen and Daugherty from 2004–2006, but were not published in Mathiasen and Daugherty (2007).

Three studies sampled a total of 2123 mountain hemlocks growing near severely infected mountain hemlocks with *Arceuthobium tsugense* subsp. *mertensianae* and reported an incidence of infection of 94% and a mean DMR of 3.5 (Mathiasen & Hawksworth 1988, Mathiasen & Daugherty 2008; Mathiasen 2011); mountain hemlock was clearly the principal host of subsp. *mertensianae*. Brewer spruce (*Picea breweriana* S. Watson) has also been reported to be severely infected by subsp. *mertensianae* and with an incidence of infection of 79% has been classified as a secondary host in northern California (Mathiasen & Daugherty 2010; Mathiasen 2011). Western white pine is occasionally infected by subsp. *mertensianae* with an incidence of infection of 30% (Mathiasen & Hawksworth 1988; Mathiasen 2011). Although there have been reports of grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) as a rare host of subsp. *mertensianae* (Mathiasen 1994; Hawksworth & Wiens 1996), these were actually based on infection of grand fir by subsp. *amabilae* (Mathiasen & Daugherty 2007). However, grand fir has also been reported to be a rare host of subsp. *tsugense* (Hawksworth & Wiens 1996), but this report has not been confirmed (Mathiasen & Daugherty 2005).

Table 8. Infection of Pacific silver fir (PSF), noble fir (NF), mountain hemlock (MH), western hemlock (WH), shore pine (SP), and western white pine (WWP) by *Arceuthobium tsugense* subsp. *tsugense*, subsp. *amabilae*, subsp. *mertensianae*, and subsp. *contortae*. Combined data for trees > 1 cm in diameter at breast height from Mathiasen & Hawksworth (1988), Wass & Mathiasen (2003), Mathiasen & Daugherty (2005, 2008), Mathiasen (2011), and Mathiasen & Daugherty (unpublished). An asterisk denotes that no data were available. [1]—Western white pine has been reported to be rarely infected by *Arceuthobium tsugense* subsp. *amabilae*, subsp. *tsugense*, and subsp. *contortae* (Gill 1935; Kuijt 1956; Hawksworth et al. 1992; Hawksworth & Wiens 1996; Wass & Mathiasen 2003; Mathiasen & Daugherty 2007).

| | *Arceuthobium tsugense* subsp. | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *amabilae* | | | *contortae* | | | *mertensianae* | | | *tsugense* | | |
| Host | N | Percent infection | Mean DMR | N | Percent infection | Mean DMR | N | Percent infection | Mean DMR | N | Percent infection | Mean DMR |
| PSF | 2130 | 95 | 3.5 | * | * | * | 127 | 0 | 0 | 2397 | 35 | 0.8 |
| NF | 1478 | 92 | 2.8 | * | * | * | 145 | 0 | 0 | 247 | 14 | 0.3 |
| MH | 2040 | 93 | 3.9 | * | * | * | 2123 | 94 | 3.5 | 165 | 27 | 0.7 |
| WH | 268 | 18 | 0.4 | 802 | 21 | 0.3 | * | * | * | 2495 | 96 | 3.1 |
| SP | * | * | * | 1576 | 97 | 4.3 | * | * | * | 77 | 1 | 0.1 |
| WWP[1] | * | * | * | * | * | * | 424 | 30 | 0.5 | 438 | 0 | 0 |

## DISCUSSION

### Host Susceptibility

The most important differences distinguishing the four subspecies of *Arceuthobium tsugense* were the result of variations in the natural susceptibility of the conifers these mistletoes parasitize in the Pacific Northwest and western Canada. The principal and most commonly infected host of subsp. *tsugense* is western hemlock (> 90% infection) throughout its geographic range, extending from northern California to southeastern Alaska (Smith & Wass 1976; Hawksworth & Wiens 1972, 1996; Mathiasen & Hawksworth 1988; Mathiasen 1994; Hennon et al. 2001; Wass & Mathiasen 2003; Mathiasen & Daugherty 2005; Muir & Hennon 2007). Presently, Pacific silver fir, noble fir, and mountain hemlock have been classified as occasional hosts of subsp. *tsugense* (Shaw 1982; Mathiasen 1994; Mathiasen & Daugherty 2005). Based on field observations and/or quantitative data, several conifers commonly found in the Pacific Northwest are also considered to be rare hosts of subsp. *tsugense,* including shore pine, western white pine, grand fir, subalpine fir, Sitka spruce (*Picea sitchensis* (Bong.) Carriére), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Gill 1935; Hunt & Smith 1978; Hawksworth & Wiens 1996; Mathiasen & Daugherty 2005; Muir & Hennon 2007). Although Smith (1974) inoculated several conifers native to the Pacific Northwest and western Canada with seeds of subsp. *tsugense* and demonstrated most of them were susceptible to infection, his data cannot be extrapolated for estimates of the natural susceptibility of those hosts to subsp. *tsugense* as the host(s) background (i.e., genetic variation) are likely not representative of the intraspecific heterogeneity within forest systems. Inoculation studies by Smith (1974) as well as those of Smith and Wass (1979), therefore, demonstrated that several conifers are at least susceptible to subsp. *tsugense* to some degree.

The host range for *Arceuthobium tsugense* subsp. *contortae* is the most distinct for all the subspecies of *A. tsugense*. Its principal host was shore pine throughout this dwarf mistletoe's limited geographic distribution in British Columbia and the San Juan Islands, Washington (Smith & Wass 1976; Wass 1976; Wass & Mathiasen 2003). This dwarf mistletoe only occasionally infected western hemlock which distinguished it from subsp. *tsugense* (Smith & Wass 1976; Wass & Mathiasen 2003). *Arceuthobium tsugense* subsp. *contortae* rarely infected western white pine and has been reported to occasionally infect Rocky Mountain lodgepole pine (*Pinus contorta* Douglas ex Loudon subsp. *latifolia* (Engelm.) Critchf.) (Kuijt 1956). However, there are no data on the natural susceptibility of many other conifers that occur in the Pacific Northwest to subsp. *contortae* because most of them do not occur within its geographic range. The lone exceptions are Douglas-fir and Sitka spruce, which are considered immune to subsp. *contortae* (Smith 1974; Wass & Mathiasen 2003).

The initial evidence of the differences in susceptibility of shore pine and western hemlock to *Arceuthobium tsugense* subsp. *contortae* was demonstrated by a series of artificial inoculation studies. Smith (1974) demonstrated that seeds of subsp. *contortae* placed on western hemlocks produced low levels of infection (1%) and no shoots, while dwarf mistletoe seeds of subsp. *tsugense* placed on western hemlocks produced higher levels of infection (22%) and 100 % of the infections produced shoots. As noted previously for subsp. *tsugense*, Smith (1974) also inoculated several conifers with seeds of subsp. *contortae* and demonstrated that most were susceptible to infection and, although his results cannot be extrapolated for estimates of the natural susceptibility of the conifers inoculated with subsp. *contortae*, these inoculation tests demonstrated that several conifers found in the Pacific Northwest and western Canada are susceptible to some degree to infection by subsp. *contortae*. The earliest field investigations of the host range of *A. tsugense* subsp. *contortae* on Vancouver Island (Smith & Wass 1976; Wass 1976) confirmed that western hemlock was much less severely-infected and, hence, less susceptible to subsp. *contortae* than shore pine. Further evidence of the relative susceptibility of shore pine and western hemlock to subsp. *contortae* was reported by Smith and Wass (1979). They demonstrated that artificial inoculations with seeds of subsp. *contortae* only produced a few infections on western hemlock (7% of the inoculations), and only a few shoots were produced by the infections. In addition, their inoculations with seeds of subsp. *tsugense* rarely caused infections on shore pine (1%), but the infections produced a larger quantity of shoots. Additional artificial inoculation experiments by Ed Wass (unpublished) using seeds of subsp. *contortae* also resulted in only a few infections on western hemlock (3%), but all of the infections produced shoots. His inoculations on shore pine with seeds of subsp. *contortae* produced many more viable infections (42%) and all of the infections produced shoots. In these same experiments, inoculations with seeds of subsp. *tsugense* on shore pine produced no infections; while 29% of the seeds inoculated on western hemlock produced infections and 93% of these produced aerial shoots (Ed Wass, unpublished). These studies provided further evidence of the low susceptibility of western hemlock to subsp. *contortae* and the low susceptibility of shore pine to subsp. *tsugense*.

The principal host of *Arceuthobium tsugense* subsp. *mertensianae* is mountain hemlock (Mathiasen & Hawksworth 1988; Hawksworth et al. 1992; Hawksworth & Wiens 1996; Mathiasen & Daugherty 2008; Mathiasen 2011); whereas, western white pine has been shown to be only an occasional host of this mistletoe (Mathiasen & Hawksworth 1988; Mathiasen 2011) (Table 8). Another host of subsp. *mertensianae* that has been demonstrated to be highly susceptible (secondary host) is Brewer spruce (Mathiasen & Daugherty 2010; Mathiasen 2011). Reports of Pacific silver fir, noble fir, and subalpine fir as principal hosts of subsp. *mertensianae* (Hawksworth et al. 1992; Hawksworth & Wiens 1996; Nickrent 2012) are incorrect; rather these hosts were infected by subsp. *amabilae* in central Oregon (Mathiasen & Daugherty 2007, 2008). Infection of Pacific silver fir by subsp. *mertensianae* has not been observed in southern Oregon where Pacific silver fir occasionally occurs near mountain hemlocks infected with subsp. *mertensianae* (Mathiasen & Daugherty 2008) (Table 8). Furthermore, reports of subsp. *mertensianae* on whitebark pine (*Pinus albicaulis* Engelm.) are based on infection of this host by limber pine dwarf mistletoe (*A. cyanocarpum* (A. Nelson ex Rydb.) Coulter & Nelson) at Crater Lake National Park, Oregon (Reif et al. 2015). The dwarf mistletoe populations on whitebark pine near McKenzie Pass, Oregon reported by Hawksworth and Wiens (1996) are likely *A. cyanocarpum* as well and requires confirmation.

The principal hosts of *Arceuthobium tsugense* subsp. *amabilae* are Pacific silver fir, noble fir, and mountain hemlock; western hemlock has been classified as an occasional host (Mathiasen & Daugherty 2007) (Table 5). Rare hosts of subsp. *amabilae* include grand fir and western white pine (Mathiasen & Daugherty 2007). The most important difference in the susceptibility of coniferous hosts to the subspecies of *Arceuthobium tsugense* are summarized in Table 8 and include: 1) western hemlock is the principal host of subsp. *tsugense* and is only infected occasionally by subsp. *amabilae*, subsp. *contortae*, and subsp. *mertensianae*; 2) western white pine is an occasional host of subsp. *mertensianae* in southern Oregon and California, and is rarely infected by the other subspecies; 3) Pacific silver fir and noble fir are the principal hosts of subsp. *amabilae*; whereas, they are only occasional hosts to subsp. *tsugense*; and, 4) shore pine is the lone principal host of subsp. *contortae*. Moreover, it must be noted that the principal hosts of the subspecies of *A. tsugense* do not overlap with the principal hosts of *A. campylopodum* as this dwarf mistletoe only parasitizes hard pines (*Pinus* L., subgenus *Pinus*). The principal hosts of *A. campylopodum* are ponderosa and Jeffrey pines; Coulter pine (*P. coulteri* D. Don) and knobcone pine (*P. attenuata* Lemmon) have been classified as secondary hosts (Hawksworth & Wiens 1996). Although it occasionally has been reported to infect gray pine (*P. sabiniana* Douglas ex D. Don) and lodgepole pine (*P. contorta* Douglas ex Loudon subsp. *murrayana* (Grev. & Balfour) Engelm. and subsp. *latifolia*), it has not been reported on shore pine. In addition, *A. campylopodum* has never been reported to infect species in the genus *Abies* Miller or *Tsuga* (Endlicher) Carriére (Hawksworth & Wiens 1972, 1996; Mathiasen & Kenaley 2016). There has been only one unconfirmed report of *A. campylopodum* on a white pine (*Pinus* L., subgenus *Strobus* Lemmon) (Hawksworth & Wiens 1996), infecting sugar pine (*P. lambertiana* Douglas) near Hammer Butte, Oregon. We suspect this report was actually based on infection of sugar pine by white fir dwarf mistletoe, *A. abietinum* Engelm. ex Munz f. sp. *concoloris* Hawksworth & Wiens, as *A. campylopodum* has never been reported on sugar pine in the Sierra Nevada Mountains where this mistletoe commonly occurs in mixed sugar pine-ponderosa pine stands. Furthermore, *A. abietinum* f. sp. *concoloris* has been reported to frequently infect sugar pine in northern California. Although we have observed *A. abietinum* f. sp. *concoloris* on grand fir on Hammer Butte, OR, infection of sugar pine by *A. campylopodum* was not found. We, therefore, suspect that *A. campylopodum* has not been reported infecting a white pine thus far.

## Morphological Characteristics

Univariate statistical analyses of female and male characters demonstrate that significant morphological differences exist among *Arceuthobium tsugense* subsp. *amabilae*, *contortae*, *mertensianae*, and *tsugense* (Tables 1 and 2). Across taxa, mean basal diameter and third internode length of male plants, mean staminate spike dimensions, mean petal length, mean anther distance to tip, and mean seed length are different among subspecies of *A. tsugense*. Multiple comparisons by female or male characters suggest also that all taxa that we recognize as subspecies of *A. tsugense* are indeed morphologically distinct from one another as well as from *A. campylopodum*. Moreover, our multivariate analyses utilizing separately 8 female or 10 male characters agree with the univariate analyses in so far as effectively classifying *A. tsugense* subsp. *amabilae*, *contortae*, and *mertensianae* to the correct taxonomic membership irrespective of host data (Table 6). Female and male plants of the latter taxa—as well as *A. campylopodum*—can also be consistently delimited to subspecies, or species for *A. campylopodum*, with as few as four and three characters, respectively (Table 3). Fruit length, third internode width, and seed dimensions (i.e., length and width) contribute most to the discrimination of female plants of subsp. *amabilae*, *contortae*, and *mertensianae* as well as *A. campylopodum*, whereas stepwise DFA using staminate spike width, third internode length, and anther diameter classified these taxa with high accuracy to their field determination. However, all female characters (N= 8) are necessary to effectively classify female *Arceuthobium tsugense* subsp. *tsugense*—resulting in nearly 70% correct classification (Tables 3 and 6). In contrast, only approximately 43% of male *A. tsugense* subsp. *tsugense* can be delimited correctly when considering all ten male characters examined herein. These results suggest that the morphologies of male and, to a lesser extent, female plants of subspecies *tsugense* are far more variable when compared to the other subspecies (Table 4). Thus, without consideration of host, the collection of female plants for taxonomic identification of subspecies *tsugense* is strongly recommended and determinations should be based on female plant height, basal diameter, width of the third internode, fruit width, and seed length as these characters clearly separate *A. tsugense* subsp. *tsugense* from its allied subspecies as well as *A. campylopodum*. The latter female morphologies have been determined previously to be of significant taxonomic value for resolving species differences among closely-related taxa within section *Campylopoda*, including members of the *A. campylopodum-occidentale* complex (Mathiasen & Kenaley 2015a, 2016) and the white pine dwarf mistletoes (Kenaley et al. 2016).

## Phenology

Periodic observations of anthesis and seed dispersal for *Arceuthobium tsugense* subsp. *amabilae* indicated that this dwarf mistletoe flowers at the same time as subsp. *tsugense*, but disperses seed approximately two weeks earlier in central Oregon. These observations of flowering and seed dispersal periodicities were conducted in 1997, 1998, 2000, 2004, and 2005 by Mathiasen & Daugherty (2007). The seed dispersal period for subsp. *amabilae* is also approximately the same as for subsp. *mertensianae* (Mathiasen & Daugherty 2007). Subspecies *contortae* disperses seed one week earlier than subsp. *tsugense* in the same locations (Wass & Mathiasen 2003). Flowering of subsp. *tsugense* averaged about one week earlier than subsp. *mertensianae* and seed dispersal averaged about 2–4 weeks later for subsp. *tsugense* than for subsp. *mertensianae* (Hawksworth et al. 1992; Hawksworth & Wiens 1996). Therefore, the length of time required for seeds of subsp. *tsugense* to mature was 13–14 months and only 12–13 months for subsp. *mertensianae*. Clearly, additional observations for flowering and seed dispersal periods are justified for all subspecies of *A. tsugense*.

### Genetic Differentiation

Current molecular evidence based on the internal transcribed spacer (ITS) region and *trnT-L-F* chloroplast DNA sequences suggested that *Arceuthobium tsugense* subsp. *tsugense* is conspecific with 11 taxa within section *Campylopoda* (Nickrent et al. 2004). However, Nickrent et al. (2004) did not include *A. tsugense* subsp. *amabilae*, *contortae*, or *mertensianae* within their phylogenetic analyses. Moreover, the plant material for subsp. *tsugense* utilized by Nickrent and colleagues was collected from western white pine in California (see Appendix 1 in Nickrent et al. 2004) that may represent subsp. *mertensianae* on western white pine, an occasional host, or possibly *A. monticola* Hawksw., Wiens, & Nickrent (western white pine dwarf mistletoe) rather than *A. tsugense* subsp. *tsugense*. Therefore, to date, the phylogenetic position(s) of *A. tsugense* subsp. *tsugense* sensu lato remains unclear and our understanding of the genetics of this group is informed only by the isozyme analyses of Nickrent and Stell (1990) or possibly by the use of subsp. *mertensianae* instead of subsp. *tsugense* (Nickrent et al. 2004). Nickrent and Stell (1990) supported the segregation of subsp. *mertensianae* from subsp. *tsugense*; however, isozyme patterns provided little evidence for the taxonomic recognition of subsp. *amabilae* and subsp. *contortae*. As previously noted, Nickrent et al. (2004) did not sample plant material for subsp. *amabilae* in their phylogenetic analyses; however, within their isozyme work, Nickrent and Stell (1990) did include one population of subsp. *amabilae* on noble fir near Mary's Peak, OR (Mathiasen & Daugherty 2007). Isozyme analyses of the Mary's Peak population indicated that it was not differentiated from subsp. *tsugense* or subsp. *contortae* and, hence, Nickrent and Stell (1990) recommended that the dwarf mistletoe on shore pine remain classified as a race of subsp. *tsugense*. Because of this recommendation and because of the distinct host ranges, and shoot size differences between the western hemlock and mountain hemlock "races" of *A. tsugense*, Hawksworth et al. (1992) described the mountain hemlock race as a separate subspecies, but also retained the shore pine dwarf mistletoe as a race. Here, we report additional morphological evidence supporting the treatment of the *A. tsugense* populations parasitizing mountain hemlock from southern Oregon to northern California as subsp. *mertensianae*. Further molecular studies are necessary in order to determine if there are additional genetic differences among the other subspecies of *A. tsugense*.

### Geographic Distribution of the Subspecies of *Arceuthobium tsugense*

The geographic distributions of *Arceuthobium tsugense* subsp. *tsugense* and subsp. *contortae* on their principal hosts are well-documented and little, if any, additional work is needed to substantiate the relatively wide geographic distribution of subsp. *tsugense* and the relatively narrow distribution of subsp. *contortae* (Hawksworth & Wiens 1972, 1996; Hennon et al. 2001; Wass & Mathiasen 2003; Muir & Hennon 2007). In contrast, the distribution of subsp. *amabilae*—which is presently thought to extend from just south of the Umpqua River to near Mount Hood in Oregon (Mathiasen & Daugherty 2007)—needs additional study in Washington. For example, a population tentatively classified as subsp. *tsugense* west of Lake Chelan at Trinity, WA should be re-examined because Pacific silver fir and subalpine fir were severely infected at this location (Mathiasen 1994). Infection of both western and mountain hemlocks at this site was much less severe and therefore, the dwarf mistletoe at this site is probably best classified as subsp. *amabilae*. The Trinity population is approximately 320 km north of the most northern known population of subsp. *amabilae* near Mount Hood, Oregon. Additional data is needed using plant morphology and host infection data from the Trinity site to verify that it does represent a population of subsp. *amabilae*. Furthermore, the distribution of subsp. *mertensianae* requires a good deal of additional study as well. At present, *A. tsugense* subsp. *mertensianae* is only thought to occur from the central Sierra Nevada Mountains to as far north as the Calapooya Mountains in southern Oregon (Mathiasen & Daugherty 2007, 2008). Severe infection of mountain hemlocks north of the Calapooya

Mountains, including those in the vicinity of McKenzie Pass and Mount Hood, Oregon are associated with infection by subsp. *amabilae* (Mathiasen & Daugherty 2007, 2008) and possibly by *A. laricis* (Piper) St. John (larch dwarf mistletoe), which has been reported to severely infect mountain hemlock in Washington and Idaho (Mathiasen 1998; Mathiasen & Kenaley 2015b). Therefore, several dwarf mistletoe populations reported on mountain hemlock in northern Oregon, Washington, and British Columbia (Hildebrand 1995; Hawksworth & Wiens 1996; Mathiasen 1998) have now been attributed to infection of mountain hemlock by *A. laricis* (Mathiasen & Kenaley 2015b, Mathiasen unpublished). These populations, particularly in Washington and southern British Columbia, need further study and require plant morphology and host infection data in order to confirm the species of mistletoe infecting mountain hemlock at these localities.

### The Classification of *Arceuthobium tsugense* under *Arceuthobium campylopodum*

Based on our analyses of morphological characters reported here and by Mathiasen and Kenaley (2015b) as well as considering the distinct host range of *Arceuthobium tsugense* subsp. *tsugense*, its classification under *A. campylopodum* as proposed by Kuijt (2012) is not supported. Furthermore, the classification of subsp. *tsugense* as a subspecies of *A. campylopodum* as proposed by Nickrent (2012, 2016) is not supported by our analyses of the morphologies of the subspecies of *A. tsugense* compared with *A. campylopodum*. Treating the subspecies of *A. tsugense* as races or forms of *A. campylopodum* subsp. *tsugense* (Rosend.) Nickrent as proposed by Nickrent (2016) ignores the morphological differences we report in this study and those reported by the investigators who described the subspecies of *A. tsugense* (Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen & Daugherty 2007). In addition, the classification proposed by Nickrent (2016) also ignores the genetic differences he and Stell detected between subsp. *tsugense* and subsp. *mertensianae* (Nickrent & Stell 1990), which led them to recommend the taxonomic classification of the latter subspecies.

Nickrent (2016), as well as his earlier treatment of section *Campylopoda* (Nickrent 2012), also misrepresents the observed and quantified host affinities of subsp. *tsugense* (Hawksworth & Wiens 1996; Mathiasen & Daugherty 2005). Nickrent (2012, 2016) included Pacific silver fir, subalpine fir, noble fir, shore pine, western hemlock, and mountain hemlock all as principal hosts of *A. campylopodum* subsp. *tsugense*, but this has been demonstrated to be incorrect (Mathiasen & Daugherty 2005, 2007) (Table 8). As noted above, Pacific silver fir, noble fir, and mountain hemlock have been shown to be only occasional hosts of subsp. *tsugense*, and therefore, are much less susceptible than the principal host designation assigned by Nickrent (2012, 2016). Furthermore, Nickrent's (2016) grouping of secondary, occasional, and rare hosts for *A. campylopodum* subsp. *tsugense* was an impractical summation in that it provided users of his treatment with no specific information on the relative susceptibility of each host. Susceptibility information is of critical importance to foresters and forest pathologists who are interested in mitigating the growth impacts dwarf mistletoes have on their hosts, or if appropriate, conserving them for wildlife habitat or because of their rarity in specific regions (Hildebrand 1995; Hawksworth & Wiens 1996; Muir & Giles 2002; Muir & Hennon 2007; Mathiasen & Kenaley 2016). For example, most of the hosts Nickrent (2016) listed as secondary-to-rare hosts were actually rare hosts of *A. tsugense* subsp. *tsugense*, but Brewer spruce is a secondary host of subsp. *mertensianae*. Nickrent (2016) listed Douglas-fir as a host of hemlock dwarf mistletoe, but it is actually immune to both subsp. *contortae* and *mertensianae*. Douglas-fir has only been reported as a rare host of *A. tsugense* subsp. *tsugense* and there is currently no information on its susceptibility to subsp. *amabilae*.

Grouping, or "lumping," together all principal hosts of the four subspecies of *A. tsugense* we recognize under the collective taxon *A. campylopodum* subsp. *tsugense* does not provide the required information needed by resource managers for their work; nor does grouping all of the less susceptible hosts into three categories without distinguishing the actual susceptibility class for each host. Forest managers are still actively managing *A. tsugense* populations in the U.S. and Canada and require accurate host range information when designing treatments to decrease or increase dwarf mistletoe infestations in forest ecosystems (Muir & Hennon 2007). Nickrent's (2016) recommendation that the subspecies of *A. tsugense* we and other investigators recognize as valid taxa be treated as host races (or forms) with no taxonomic status is impractical; if these dwarf mistletoe populations have not been given taxonomic status, it is possible they will not be recognized by foresters, botanists, wildlife biologists, or conservationists interested in their management or preservation (Baldwin 2000; Mathiasen & Kenaley 2016). Therefore, we recommend that resource managers working with these parasitic plants not adopt Nickrent's (2012, 2016) classifications of *A. tsugense* as a subspecies of *A. campylopodum*. It is much more practical and useful to recognize the classification of the dwarf mistletoe populations parasitizing western hemlock as a principal host as *A. tsugense* and, therefore, the populations on mountain hemlock, Pacific silver fir, noble fir, and shore pine as subspecies of *A. tsugense*. The latter working classification is strongly supported by the present study, detailing the morphological differences among these subspecies using robust statistical procedures. This classification was also supported by the clear differences in their host affinities reported by several investigators and summarized here.

Other problems that arise from Nickrent's (2016) treatment of *Arceuthobium tsugense* as a subspecies of *A. campylopodum* can be seen in his keys and diagnostic descriptions. For example, in his key, the couplet for *A. campylopodum* subsp. *tsugense* (pg. 429) has the maximum length of stems as 13 cm; but, stems of *A. tsugense* subsp. *tsugense* and subsp. *amabilae* can reach 18–19 cm in length (Mathiasen & Daugherty 2007, Mathiasen & Kenaley 2017). Furthermore, Nickrent (2016) has the maximum length of third internodes as 16 cm (mm, sic), but third internodes of subsp. *amabilae* can reach 26 mm (Mathiasen & Daugherty 2007). These errors limit the usefulness of his keys. In addition, his diagnostic description of *A. campylopodum* subsp. *tsugense* has several errors if our morphological data is used in lieu of that summarized in Hawksworth and Wiens (1996) including measurements for stem and third internode length, mean staminate flower diameter, and fruit dimensions (see Nickrent 2016 and compare with Table 2).

Because Nickrent (2016) has grouped all of the taxa we recognize as subspecies of *A. tsugense* under *A. campylopodum*, using his keys and descriptions for these dwarf mistletoe populations would be essentially untenable. Applying the information in his treatment would seldom lead to the correct classification or field determination of the populations of *A. tsugense* from central Oregon through Washington where subsp. *tsugense* and subsp. *amabilae* predominate. Likewise, *A. tsugense* subsp. *mertensianae* is the most common dwarf mistletoe on mountain hemlock in southern Oregon and northern California and its circumscription under *A. campylopodum* subsp. *tsugense* would significantly complicate the determination of this genetically distinct taxon within the region as the hosts listed in Nickrent (2016) artificially dilutes the demonstrated host specificity of subsp. *mertensianae* to include immune and less susceptible hosts.

Nickrent (2012) contended that seven species of *Arceuthobium* in ser. *Campylopoda* (Hawksworth & Wiens 1996) are not host specific and could be considered generalists in that they parasitize more than one host species as a principal host. However, his analysis of host specialization was based on his classification of taxa in ser. *Campylopoda* as subspecies of *A. campylopodum*. Therefore, his analysis did not include the subspecies we recognize under *A. tsugense* or *A. abietinum* Engelm. ex Munz. Following our classification, subsp. *tsugense*, subsp. *contortae*, and subsp. *mertensianae* have only one principal host and subsp. *amabilae* has three (Table 9); not the six principal hosts Nickrent (2012) assigned to *A. campylopodum* subsp. *tsugense*. In the classification for *A. abietinum* we follow, *A. abietinum* Engelm. ex Munz f. sp. *magnificae* Hawksworth & Wiens has one principal host, *A. abietinum* Engelm. ex Munz subsp. *wiensii* Mathiasen & C. Daugherty has two, and *A. abietinum* f. sp. *concoloris* has three (Table 9). So the special forms and subspecies of *A. abietinum* we recognize have one, two, or three principal hosts, not the four principal hosts Nickrent (2012) assigned to his *A. campylopodum* subsp. *abietinum* (Engelm.) Nickrent. However, Nickrent later used principal hosts as one of the most important characters to identify species and subspecies of *Arceuthobium* in his diagnostic keys (Nickrent 2016). His use of host specificity for the diagnoses of taxa is in stark contrast to his assertion that dwarf mistletoes in ser. *Campylopoda* are not host-specific parasites.

Nickrent (2012) also speculated that the number of occasional and rare hosts parasitized by taxa in ser. *Campylopoda* supported his argument that several of the species recognized by Hawksworth and Wiens (1996) have a propensity towards being generalists. However, it has long been known that many species of *Arceuthobium* cross infect hosts other than their principal hosts to varying degrees (Weir 1915; Gill 1935: Hawksworth & Wiens 1972) and dwarf mistletoes are considered by other investigators to be host-specific

Table 9. Principal hosts of *Arceuthobium laricis* and *monticola,* subspecies of *A. microcarpum* and *A. tsugense*, and subspecies and special forms of *A. abietinum*. Based on data in Hawksworth and Wiens (1996), Wass and Mathiasen (2003), Mathiasen and Daugherty (2005, 2007, 2009, 2010), Scott and Mathiasen (2009), and Mathiasen (2011).

| *Arceuthobium* | **Principal host(s)** |
|---|---|
| *A. abietinum* subsp. *wiensii* | *Abies magnifica, Picea breweriana* |
| *A. abietinum f. speciales magnificae* | *Abies magnifica* |
| *A. abietinum f. speciales concoloris* | *Abies concolor, Abies durangensis, Abies grandis* |
| *A. laricis* | *Larix occidentalis* |
| *A. microcarpum* subsp. *microcarpum* | *Picea engelmannii, Picea pungens* |
| *A. microcarpum* subsp. *aristatae* | *Pinus aristata* |
| *A. monticola* | *Pinus monticola, Picea breweriana* |
| *A. tsugense* subsp. *tsugense* | *Tsuga heterophylla* |
| *A. tsugense* subsp. *amabilae* | *Abies amabilis, Abies procera, Tsuga mertensiana* |
| *A. tsugense* subsp. *contortae* | *Pinus contorta* subsp. *contorta* |
| *A. tsugense* subsp. *mertensianae* | *Tsuga mertensiana* |

mistletoes in that they primarily parasitize closely-related species as principal hosts (Norton & Carpenter 1998). Only four species of *Arceuthobium* recognized by Hawksworth and Wiens (1996) and Mathiasen and Kenaley (2016a) parasitize principal hosts in more than one genus of the Pinaceae: 1) *Arceuthobium abietinum—Abies* and *Picea*; 2) *A. microcarpum* (Engelm.) Hawksworth & Wiens—*Picea* and *Pinus*; 3) *A. monticola—Picea* and *Pinus*, and 4) *A. tsugense—Abies*, *Pinus*, and *Tsuga* (Table 9). The large majority of dwarf mistletoes recognized by Hawksworth and Wiens (1996) parasitize principal hosts in the same genus, particularly *Pinus* spp , and are most often limited to either hard or white pines with no or limited cross infection between subgenera *Pinus* and *Strobus.* Several Mexican taxa of *Arceuthobium* parasitize many more than three or four principal hosts, some as many as 12, but the hosts are all pines (Hawksworth & Wiens 1996). Therefore, the parasitism of 1–3 closely-related principal hosts by most of the taxa in ser. *Campylopoda*, including subspecies of *A. tsugense*, supports our interpretation that they are relatively host-specific parasites and this perspective is shared by other investigators (Hawksworth & Wiens 1996, Norton & Carpenter 1998). However, several dwarf mistletoes parasitize conifers as occasional or rare hosts in genera other than that of their principal hosts (Hawksworth & Wiens 1996) and some of these are among the most distinctive species of *Arceuthobium*: e.g. *A. americanum*, *A. douglasii* Engelm., and *A. pusillum* Peck. In addition, these taxa parasitize more than one principal host, but they are still considered as examples of relatively host-specific mistletoes (Hawksworth & Wiens 1996).

Nickrent (2012) suggested that an ancestral species with a wide host range may have given rise to new taxa in ser. *Campylopoda* with more specialized host affinities. The extant taxa that have the broadest host ranges in that they parasitize to some degree (principal to rare hosts) several genera of the Pinaceae are *Arceuthobium abietinum*, *A. cyanocarpum*, *A. laricis*, and *A. tsugense* (Hawksworth & Wiens 1996). However, Nickrent et al. (2004) suggested *A. blumeri* A. Nelson was probably the most basal species in sect. *Campylopoda,* but *A. blumeri* only parasitizes *Pinus strobiformis* Engelm. in southern Arizona and northern Mexico; therefore, it cannot be considered a generalist. Although Mathiasen (1982), Hawksworth and Wiens (1996), and Nickrent (2012) included *P. ayacahuite* Ehrenb. ex Schltdl. as a host of *A. blumeri*, the present classification of the hosts of *A. blumeri* in northern Mexico are considered to represent only *P. strobiformis* (Frankis 2009; Moreno-Letelier & Piñero 2009; Kenaley et al. 2016). Therefore, *A. blumeri* is one of the most host specific of the taxa in ser. *Campylopoda* and, has clearly diverged from its generalist common ancestor. Thus, it is difficult to broadly characterize/hypothesize the evolution of host affinities among dwarf mistletoes, from generalist to host specific, in view of present day molecular data. However, *A. tsugense* appears to still be evolving and the subspecies that have been described thus far support this concept and may indicate that *A. tsugense* populations will continue to radiate onto additional hosts via host-switching in the future.

Our morphological analyses of the subspecies of *Arceuthobium tsugense* demonstrate that subsp. *contortae* is morphologically quite distinct from the three other subspecies as well as from *A. campylopodum* (Tables 2, 5, and 6; Fig. 5). The results of the DFA in particular suggest that subsp. *contortae* can be classified as a separate species. Furthermore, its distinct host range also support this conclusion. Of the four subspecies of *A. tsugense* studied here, it is the only taxon whose principal host is a pine and it only occasionally infects western hemlock (Smith & Wass 1976; Wass & Mathiasen 2003). Further molecular studies using more variable markers than just ITS and *trnT-L-F* gene regions are needed to ascertain if there are sufficient genetic differences between subsp. *tsugense* and subsp. *contortae* which would support raising the rank of the latter subspecies to species.

### Subspecies of *Arceuthobium*

Giving taxonomic status to the populations of *Arceuthobium tsugense* with a few significantly different morphological characters and different host affinities at the subspecific level is consistent with the classification of the other subspecies of *Arceuthobium* (Hawksworth & Wiens 1972; Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen 2007, 2008; Mathiasen & Daugherty 2007, 2009; Scott & Mathiasen 2009). Differences in plant size and host range have been the principal characters used to separate subspecies of *Arceuthobium* and these are the same characteristics that distinguish the subspecies of *Arceuthobium tsugense* (Tables 2 and 10). The classification of the subspecies of *Arceuthobium tsugense* is relatively consistent with the taxonomic framework for subspecies established by Hawksworth and Wiens' 1996 monograph of *Arceuthobium* in which they stated "geographically restricted populations delimited by a few relatively small but consistent variations are best classified as subspecific units." However, because the geographic distributions of some of the subspecies of *A. aureum* Hawksworth & Wiens and *A. vaginatum* (Wildenow) Presl overlap (Hawksworth & Wiens 1996; Mathiasen 2008), subspecies of *Arceuthobium* do not consistently meet the "geographically restricted" criterion initially adopted by Hawksworth and Wiens (1972, 1996). While the morphological differences we detected between the subspecies of *A. tsugense* appear to be minor differences, with the possible exception of subsp. *contortae*, the host ranges for all of the subspecies are distinct. Furthermore, there are some slight differences when the subspecies flower (Hawksworth & Wiens 1996; Wass & Mathiasen 2003; Mathiasen & Daugherty 2007). Although the subspecies of *A. tsugense* are delimited by a small number of morphological and physiological differences, the geographic distribution of subsp. *amabilae* does overlap with the distribution of subsp. *tsugense* in central Oregon and the distributions of subsp. *amabilae*, subsp. *mertensianae* and subsp. *tsugense* nearly overlap near Crater Lake, Oregon. Therefore, these subspecies do not adhere strictly to the "geographically restricted" criterion suggested by Hawksworth and Wiens either. At present, the classification of subspecies under *A. abietinum*, *A. aureum*, *A. hondurense* Hawksworth & Wiens, *A. microcarpum*, *A. tsugense*, and *A. vaginatum* is relatively consistent in that the subspecies are distinguished by a few morphological differences and by their host ranges. However, the classification of subsp. *contortae* at the rank of species should be considered because our morphometric analyses indicate it is morphologically more distinct from *A. tsugense* subsp. *tsugense* than the other subspecies and its parasitism of shore pine as its only principal host also supports this recombination. Furthermore, where subsp. *tsugense* and subsp. *contortae* are sympatric in British Columbia they can be identified by their morphological characteristics and differential parasitism of western hemlock versus shore pine (Smith & Wass 1976; Wass & Mathiasen 2003).

The taxonomic classification of dwarf mistletoe populations as species or subspecies ultimately comes down to the perspectives and judgments of the investigators studying these parasitic plants. As with other genera of plants that have morphologically reduced vegetative and/or floral characteristics (e.g. *Carex* spp.), there will undoubtedly be multiple interpretations and conclusions reached by plant taxonomists regarding their classification. But despite the differing taxonomic interpretations by Kuijt (2012) and Nickrent (2012, 2016), we will continue to maintain that the most practical classification of *A. tsugense* follows the interpretations of Hawksworth et al. (1992), Wass and Mathiasen (2003), Mathiasen and Daugherty (2007), and Mathiasen and Kenaley (2016).

Table 10. Principal morphological and physiological differences between *Arceuthobium tsugense* subsp. *amabilae* (PSFDM), subsp. *contortae* (SPDM), subsp. *mertensianae* (MHDM), and subsp. *tsugense* (WHDM). Plant heights in cm and all other characters in mm. [1]—Host susceptibility system follows Hawksworth and Wiens (1972, 1996). Host classifications for PSFDM are based on data from field observations. Host classifications for WHDM are based on data presented by Mathiasen and Daugherty (2005) and Shaw (1982). Host classifications for MHDM are based on data from Mathiasen and Hawksworth (1988) and from field observations. Earlier classifications of Pacific silver fir and noble fir as principal hosts of MHDM are based on the classification of the PSFDM as the MHDM in Oregon (Mathiasen 1994; Hawksworth and Wiens 1996).

| | *Arceuthobium tsugense* subsp. | | | |
|---|---|---|---|---|
| Character(s) | *amabilae* | *contortae* | *mertensianae* | *tsugense* |
| **Mean plant height** | | | | |
| Male | 9.4 | 5.6 | 5.7 | 7.8 |
| Female | 10.6 | 6.6 | 6.1 | 8.0 |
| **Mean Basal Diameter** | | | | |
| Male | 3.1 | 2.8 | 1.9 | 2.6 |
| Female | 3.4 | 3.3 | 2.2 | 2.7 |
| **Mean Third Internode Width** | | | | |
| Male | 1.9 | 1.8 | 1.3 | 1.6 |
| Female | 2 | 1.7 | 1.4 | 1.6 |
| **Mean staminate spike length** | 9.5 | 12.6 | 6.9 | 10.8 |
| **Mean staminate spike width** | 1.3 | 3.4 | 1.2 | 1.6 |
| **Mean flower diameter** | | | | |
| 3- and 4-merous combined | 3.4 | 4.3 | 2.7 | 3.5 |
| **Mean fruit length** | 4.7 | 4.6 | 3.8 | 4.4 |
| **Male plant color** | Green-brown/ yellow-green/green | Green-brown | Yellow-green/ green-brown | Yellow-green |
| **Female plant color** | Green/green-brown | Green-brown | Green/green-brown | Yellow-green /purple |
| **Host Susceptibility**[1] | | | | |
| Pacific Silver Fir | Principal | Unknown | Immune | Occasional |
| Western Hemlock | Occasional | Occasional | Occasional | Principal |
| Mountain Hemlock | Principal | Unknown | Principal | Occasional |
| Noble Fir | Principal | Unknown | Unknown | Occasional |
| Western White Pine | Rare | Rare | Occasional | Rare |
| Shore pine | Unknown | Principal | Unknown | Rare |
| **Peak seed dispersal** | Two weeks earlier than WHDM | One week earlier than WHDM | Two weeks earlier than WHDM | Two weeks later than PSFDM and MHDM |
| **Peak flowering** | | | One week later than WHDM | One week earlier than MHDM |

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