



The *Luzula comosa* complex (*Luzula* section *Luzula*, Juncaceae) in western North America

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Abstract

Field and herbarium study of *Luzula comosa* and its allies revealed two taxa in western North America that were overlooked in recent years but are distinct and best treated as species. *Luzula cascadiensis*, once considered a variety of *Luzula campestris*, is elevated to species rank. It inhabits montane wetlands from southern Washington to California, east to Idaho and Montana. It is distinguished from *Luzula comosa* by its elongate horizontal rhizomes, usually darker tepals, and wetter habitats. *Luzula macrantha* is raised to species rank and separated from *Luzula subsessilis* by differences in inflorescence architecture as well as the length of the tepals, styles, and anthers. *Luzula macrantha* is found in dry forest and openings from southern British Columbia to California. Lectotypes are designated for *Luzula comosa* var. *laxa* and *Luzula comosa* var. *congesta*. Descriptions, distribution maps, synonymy, a key, and illustrations are provided for members of the group.

Keywords: new species, Canada, United States

Luzula de Candolle (1805: 158) sect. *Luzula* (Kirschner *et al.* 2002) consists of cespitose or rhizomatous perennial graminoids with obtuse, slightly swollen leaf tips. Their inflorescences are spike-like clusters of many flowers (rarely three), arranged in umbel-like or head-like inflorescences. The flowers are small, with six scarious, brown, dark purple, or black tepals, and six stamens. The capsules contain three seeds, each with a basal aril (caruncle). Members of *Luzula* sect. *Luzula* grow in Eurasia, North and South America, Australia, and New Zealand. The section is taxonomically challenging (Kirschner 1990).

In this study we treat four native species of *Luzula* sect. *Luzula*, one with two varieties. These morphologically similar taxa can be referred to as the *L. comosa* Meyer (1823: 21) complex. The complex includes all members of *Luzula* sect. *Luzula* in California, Oregon and Washington, with the exception of *L. campestris* and *L. multiflora*, which are generally distinguished by their consistently denser spikes. Species included in the complex are *L. comosa* with two varieties, *L. subsessilis* (Watson 1880: 203) Buchenau (1898: 290), and two taxa we raise to the rank of species, *L. cascadiensis* and *L. macrantha*.

Lacking access to type specimens or a coherent treatment, North American botanists have been troubled by the group for more than a century. Over a dozen different names have been applied to these five taxa (Table 1). Sometimes all have been treated as *L. comosa* (Swab 1993, 2000) or *L. campestris* (Linnaeus 1753: 329) de Candolle (1805: 161; *e.g.*, Abrams 1940). All but one have been treated as *L. multiflora* (Ehrhart 1790: 14) Lejeune (1811: 169; *e.g.*, Peck 1961) or *L. campestris* var. *congesta* (Thuillier 1799: 178) Bicheno (1819: 334; *e.g.*, Hitchcock & Cronquist 1973). Clearly this was a group in need of revision.

Good progress in interpreting Pacific North American taxa came from studies of euploidy and agamaploidy in *Luzula* sect. *Luzula* (Nordenskiöld 1951, 1956, 1971). However, the taxonomic confusion of the day limits the current usefulness of Nordenskiöld's work. Not all of the relevant material used in Nordenskiöld's chromosome studies could be safely equated with the native taxa treated below. We attempted to check the identification of her voucher specimens, but some could not be found when we attempted to borrow them from UPS. Because of the importance of polyploidy and agamaploidy in understanding the evolution of the *Luzula comosa* and similar species (Kirschner 1992a), a new karyological study should be carried out using seeds from recently collected herbarium vouchers.

TABLE 1. Names applied historically to the five taxa recognized here in the *Luzula comosa* complex in western North America. Taxa not cited elsewhere in the text: *L. campestris* var. *frigida* Buchenau (1898: 284); *L. campestris* var. *multiflora* (Ehrhart 1790: 14) Čelakovský (1867: 85); *L. multiflora* var. *congesta* (Thuillier 1799: 178) Koch (1837: 734); *L. subcongesta* (Watson 1880: 202) Jepson (1921: 258)

Reference	Geographic Area	<i>L. cascadiensis</i>	<i>L. comosa</i> var. <i>comosa</i>	<i>L. comosa</i> var. <i>laxa</i>	<i>L. macrantha</i>	<i>L. subsessilis</i>
Kirschner 2012	California	<i>L. comosa</i> var. <i>laxa</i>	<i>L. comosa</i> var. <i>comosa</i>	<i>L. comosa</i> var. <i>laxa</i>	<i>L. subsessilis</i>	<i>L. subsessilis</i>
Kirschner <i>et al.</i> 2002	North America	<i>L. campestris</i> var. <i>columbiana</i>	<i>L. comosa</i> var. <i>comosa</i>	<i>L. comosa</i> var. <i>laxa</i>	<i>L. subsessilis</i>	<i>L. subsessilis</i>
Česka & Kirschner 2001	British Columbia		<i>L. comosa</i> var. <i>comosa</i>	<i>L. comosa</i> var. <i>laxa</i>	<i>L. subsessilis</i>	<i>L. subsessilis</i>
Swab 2000	North America	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>
Swab 1993	California	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>
Welsh <i>et al.</i> 1993	Utah		<i>L. campestris</i> var. <i>multiflora</i>			
Weber 1990	Colorado		<i>L. comosa</i>			
Coffey 1986	Great Plains		<i>L. multiflora</i>			
Martin & Hutchins 1980	New Mexico		<i>L. multiflora</i>			
Scoggan 1978	Canada		<i>L. multiflora</i> subsp. <i>comosa</i>	<i>L. multiflora</i> subsp. <i>multiflora</i>		
Cronquist 1977	Intermountain Region	<i>L. campestris</i> var. <i>multiflora</i>	<i>L. campestris</i> var. <i>multiflora</i>	<i>L. campestris</i> var. <i>multiflora</i>		
Hitchcock & Cronquist 1973	Pacific Northwest	<i>L. campestris</i> var. <i>frigida</i>	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>congesta</i>
Munz & Keck 1965	California	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. comosa</i>	<i>L. subsessilis</i>	<i>L. subsessilis</i>
Harrington 1964	Colorado		<i>L. multiflora</i>			
Peck 1961	Oregon	<i>L. subcongesta</i>	<i>L. multiflora</i> var. <i>congesta</i>	<i>L. multiflora</i> var. <i>comosa</i>	<i>L. multiflora</i> var. <i>congesta</i>	<i>L. multiflora</i> var. <i>congesta</i>
Kearney <i>et al.</i> 1960	Arizona		<i>L. multiflora</i>			
Moss 1959	Alberta		<i>L. multiflora</i>			
Davis 1952	Idaho	<i>L. comosa</i> var. <i>congesta</i>	<i>L. comosa</i> var. <i>comosa</i>	<i>L. comosa</i> var. <i>comosa</i>		
Abrams 1940	Pacific States	<i>L. campestris</i>	<i>L. campestris</i>	<i>L. campestris</i>	<i>L. campestris</i>	<i>L. campestris</i>
Tidestrom 1925	Nevada, Utah		<i>Juncoides campestris</i>			
Fernald & Wiegand 1913	North America	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>comosa</i>	<i>L. campestris</i> var. <i>congesta</i>	<i>L. campestris</i> var. <i>congesta</i>
					<i>macrantha</i>	<i>comosa</i>

A world-wide revision of the genus *Luzula* (Kirschner *et al.* 2002) provided a welcome summary that typified several Pacific Northwest taxa and provided keys, maps, and discussion of some of the remaining taxonomic problems in the genus. One of the regions recognized as needing further revision was in western North America (Kirschner *et al.* 2002). Results of the revision are presented here.

Methods and Materials

Applying a modern treatment (Kirschner *et al.* 2002) to *Luzula* specimens from OSC, ORE, WILLU, and WTU revealed that many of the specimens were misidentified and that some did not fit into published taxa. Therefore, we reviewed more than 2400 herbarium specimens of the *L. comosa* complex from over 30 herbaria (ASC, ASU, BH, BRY, CAS, CHSC, COLO, CU, DS, GH, ID, JEPS, K, MO, MONTU, NY, ORE, OSC, PH, POM, PR, RM, RSA, SOC, UBC, UC, US, V, W, WILLU, WS, WTU, and WTUH; herbarium acronyms from Thiers continually updated). Only specimens that we saw were cited or used to produce maps.

Specimens were classified according to the taxon concepts in Kirschner *et al.* (2002), with their *L. subsessilis* divided into two groups that appeared to be distinct taxa. Fifty or more specimens for each of the five putative taxa we recognized in the *L. comosa* complex were measured to establish the normal range of variation (and occasional outlying measurements, presented in parentheses) for each taxon (Table 2). The method used was a traditional taxonomic approach; many mature specimens were measured, until it was clear that additional measurements did not move the range of measurements. If a specimen was odd in some way, it was measured completely. A running tally of the number of specimens measured was kept, but which specimens they were was not recorded.

TABLE 2. A morphological comparison of members of the *Luzula comosa* complex in western North America, based on measurements of 50 herbarium specimens of each taxon. Infl = inflorescence shape; P = long-peduncled proximal spike, from leaf axil; T = a terminal head; U = umbellate. Dried seed measurements are length (including aril) × width. The dried fleshy aril measurement does not include the fibrillose base. Parentheses = rare, extreme measurements.

Species	Stem base	Infl	Tepal color	Length (mm)				Aril
				Tepal	Style	Anther	Seed	
<i>L. cascadiensis</i>	± Horizontal rhizomes	U (T)	Dark (pale)	(1.7)2.3–3.3(3.6)	(0.1)0.2–0.8(1.1)	(0.35)0.4–1.2	(0.95)1.1–1.6 × 0.5–0.75(0.9)	(0.15)0.2–0.4
<i>L. comosa</i> var. <i>comosa</i>	Bulbs	T (P)	Pale (dark)	2.3–3.5(4)	(0.2)0.4–0.8	0.5–0.9(1.1)	(1.1)1.2–1.6(1.85) × 0.6–0.9	0.15–0.6
<i>L. comosa</i> var. <i>laxa</i>	Bulbs	U	Pale	(2)2.2–.9(4.2)	0.2–0.9(1.1)	0.5–0.9(1.1)	(1.1)1.2–2.1 × (0.6)0.65–1.1(1.2)	(0.2)0.3–0.6(0.7)
<i>L. macrantha</i>	Bulbs	U	Dark	(3.4)3.6–5.8(6.1)	(0.7)0.8–2.3	(1.1)1.2–2.8(3.1)	(1)1.3–2 × (0.7)0.8–1.3	0.2–0.4(0.6)
<i>L. subsessilis</i>	Bulbs	T, P	Dark	2.1–3.7(4)	0.1–0.7	0.4–1.1(1.3)	(0.9)1.2–1.85 × 0.7–1.1	0.2–0.6

Classification of members of the *L. comosa* complex were compared in Table 1, using 21 relevant major floras (Abrams 1940, Češka & Kirschner 2001, Coffey 1986, Cronquist 1977, Davis 1952, Fernald & Wiegand 1913, Harrington 1964, Hitchcock & Cronquist 1973, Kearney *et al.* 1960, Kirschner 2012, Kirschner *et al.* 2002, Martin & Hutchins 1980, Moss 1959, Munz & Keck 1965, Peck 1961, Scoggan 1978, Swab 1993, Swab 2000, Tidestrom 1925, Weber 1990, Welsh *et al.* 1993).

Results

Despite some overlap in measurements, each taxon in the *Luzula comosa* complex has its own distinctive combination of traits (Table 2; discussions of each taxon, below). The horizontal rhizomes of *L. cascadiensis* are unique in this complex. Sympatric *L. macrantha* and *L. subsessilis* both have dark tepals but differ in the length of anthers and tepals (Table 2). In addition, *L. macrantha* typically has a more open inflorescence. More detailed results are included in the taxonomic treatment below.

The five members of the *L. comosa* complex were treated as one to four different taxa (Table 1). When they were treated as a single taxon, they were called *L. comosa* or *L. campestris*. All the dark-flowered taxa were united as *L. multiflora*. Unique *L. cascadiensis* was often held separate from the other species but confused with rhizomatous Eurasian species. Only Fernald & Wiegand (1913) distinguished the sympatric taxa we recognize as *L. macrantha* and *L. subsessilis*.

Discussion

In this paper we provide new names at the rank of species for two members of the *Luzula comosa* complex, which now includes four species and two varieties. One species was long confused with, and included in, *L. subsessilis*. Another species was originally described as a variety of *L. campestris*, and ignored by regional authors ever since. We also carefully circumscribe the two varieties of *L. comosa* to distinguish them from similar taxa. Our choices of lectotypes serve to stabilize and clarify the synonymy and taxonomy of the complex.

Throughout most of their range, well-developed individuals of the five taxa included here can be readily distinguished. However, in central California the inflorescences of *Luzula comosa* var. *laxa* Buchenau (1906: 83) seem to vary in color more than usual, and additional characters must be examined carefully for correct identification. Some individuals of *L. comosa* var. *comosa*, though separated by phenology and habitat, can look similar to *L. subsessilis*. Other problems complicated identifications. We observed that depauperate plants may have unusually condensed inflorescences. Those growing in shade may have unusually small flower parts. Cespitose plants growing where soil accumulates may form short vertical rhizomes, leading to confusion with *L. campestris* or other species with well-developed, horizontal rhizomes. Hybridization is possible in *Luzula* sect. *Luzula*, particularly between plants with the same chromosome number (Nordenskiöld 1956, Kirschner 1991), but potential hybrids were rarely observed during this study.

To permit accurate identification, we provided a key and illustrations showing natural variation, which was not addressed in previous works (Fernald & Wiegand 1913, Abrams 1940, Munz & Keck 1965, Swab 2000). The key accommodates some rarely seen but confusing forms.

Luzula sect. *Luzula* includes a complex of several closely related Eurasian and North American species, among them the amphi-Atlantic *L. multiflora*. In the course of this study we found that the *L. multiflora* complex is represented in the Pacific Northwest by what appear to be multiple or highly variable native taxa in undisturbed, often remote habitats, as well as other populations in disturbed and agricultural settings, which may represent introductions. The existing subspecific names for *L. multiflora* may not parse this variation in a useful way (Coffey 1970). However, revising this circumboreal complex was beyond the scope of this study. More field research and chromosome analyses are needed to resolve the relationships of these populations to each other and to *L. kobayashii* Satake (1932: 186) of the north Pacific. In the identification key, we used the name *L. multiflora* broadly and made no attempt to apply the current subspecific taxonomy, which we suspect is inadequate. However, different measurements are reported for *L. multiflora* in different parts of the key, as appropriate.

Taxonomy

1. *Luzula cascadiensis* Zika, *nom et stat. nov.* (Figs. 1–2, 3A, C).

Luzulae comosae affinis sed rhizomatibus horizontalibus elongatis, tepalis saepissime obscurioribus et habitatione montana turfosa vel riparia notabilis.

Type:—UNITED STATES. Washington: Skamania County, near channels in peaty fen, SE end of South Prairie, 910 m, 9 July 2011, *P. F. Zika* 25552 (holotype WTU, isotypes CAS, GH, K, MICH, MO, NY, OSC, PRA, RSA, UC, US).

Luzula campestris (Linnaeus 1753: 329) de Candolle (1805: 161) var. *columbiana* St. John (1936: 219).

Type:—UNITED STATES. Oregon: Hood River County, Government Camp, Mt. Hood, open woods, 4500 ft [1372 m], 3 July 1926, *C. English* 83 (holotype WS).

Perennial herbs, tufted or solitary, with elongate delicate or coarse horizontal and fragile rhizomes, often fibrous; stems (10)22–70 cm tall, usually exceeding the leaves, not bulbous-thickened basally; basal sheaths pale brown. Leaves 1–5,

distributed on the proximal 2/3 of the stems; blades herbaceous, 40–200 × 1.3–5.7 mm, flat, becoming channeled near swollen, blunt, pale or brownish apex, margins spreading-hairy, the hairs becoming sparse with age, the margins (at 40×) papillose-serrate; leaf sheaths tight, densely long white hairy at V-shaped apex. Vegetative rosettes with blades to 230 × 1.5–5.7 mm. **Inflorescences** 1–13 × 1–5.5 cm, open umbels of spikes, rarely compound, the rays stiffly erect to spreading-ascending, rarely somewhat arching, occasionally congested into a single or lobed head, with 1–7 spikes. Spikes sessile or on peduncles 1–11.2 cm, spikes (3)5–11 × 4–9 mm, 3–26 flowered, dense or loose basally. Proximal inflorescence bract green or reddish, shorter than to longer than the inflorescence, apices swollen, blunt, and discolored. Branches subtended by inconspicuous scarious, greenish, or reddish bracts, apices acuminate. Flowers subtended by three scarious acuminate to acute bracteoles, margins erose to sparsely hairy, becoming increasingly dissected with age. **Tepals** 6, (1.7)2.3–3.3(3.6) mm, dark brown or blackish, less commonly mid-brown or pale, stamens 6, filaments (0.3)0.4–0.6(0.7) mm, anthers yellow, linear, (0.35)0.4–1.2 mm, styles straight, persisting, easily broken, (0.1)0.2–0.8(1.1) mm. **Capsules** obovate-trigonous, 1.8–2.4 × 1–1.5 mm, apices acute or blunt; with three seeds (0.95)1.1–1.6 mm long (including basal aril) × 0.5–0.75(0.9) mm, fleshy pale aril (0.15)0.2–0.4 mm long, not including the fibrillose base.

Nordenskiöld (1951, 1956) reported *Luzula cascadiensis* (as *L. campestris* var. *columbiana*) as a diploid with $2n = 12$.

Paratypes:—UNITED STATES. **California**: Butte County, Cherry Hill Meadow, 1414 m, 21 July 1983, *Morey 496* (CHSC); 1.6 km SW of Jones Meadow, 5 July 1987, *Janeway 2441* (CAS, CHSC); Butte Meadows, 1326 m, 29 July 1988, *Janeway 3104* (CHSC); 1.6 air km NW of Philbrook Reservoir, 1676 m, 29 July 1992, *Ahart 6895* (CHSC); 2.4 air km NE of Jones Meadow, 1886 m, 28 September 2010, *Ahart 17260* (CHSC, RSA, WTU); 2.1 air km S of Quartz Hill, 1000 m, 5 August 2011, *Zika 25714 et al.* (WTU); Colusa County, NE slope West Peak, cirque area between peaks, Snow Mt., 2012 m, 16 September 1980, *Heckard & Hickman 5457* (JEPS); El Dorado County, El Dorado National Forest, 13 June 2003, *Kemper 184* (ID); Benwood Meadow, 1.6 km S of Echo summit, 26 July 2010, *Christie 1918* (ASC); Fresno County, South Fork San Joaquin River, 2499 m, 18 July 1952, *Raven 4466* (RM); Glenn County, 4.8 air km NW of Black Butte, 1790 m, 3 July 2011, *Zika 25505* (WTU); Humboldt County, McKay Camp, South Fork Mountain, 1676 m, 25 July 1950, *Harris 7626 & Tracy* (GH); Inyo County, Rock Creek Lake Basin, W shore Ruby Lake, 3399 m, 6 August 1939, *Pierson 12778* (CAS); Kern County, near Tiger Flat, E side Sunday Peak, 1981 m, Greenhorn [Range], 23 September 1970, *J. T. Howell 47328* (CAS); Portuguese Pass Road, 9 km N of Greenhorn Pass, 2088 m, Greenhorn Range, 21 June 1957, *Twisselmann 3688* (CAS); Lake County, near Snow Mountain, 8 August 1979, *Dibble & Griggs 170* (CHSC); Los Angeles County, San Gabriel Mountains, SW side Mt. Waterman, 2134 m, 15 July 1967, *Wheeler 10063* (RSA); Mono County, 0.3 air km NW of Upper Sardine Lake, near Bloody Canyon Trail, E of Mono Pass, 3170 m, 10 August 2012, *Zika 26089 et al.* (OSC, PRA, WTU); Slate Creek Basin, Cabin Creek, 3080 m, 1 September 1937, *Keck 4708* (DS [2 sheets], UC); [seed from] Cabin Creek, 3048 m, 8 September 1948, *Sharsmith 5700* (UPS [chromosome voucher $2n = 12$]); Cold Water Campground, 2743 m, 3 August 1971, *Thorne 41153 et al.* (RSA); Leavitt Meadows to Piute Meadows along main trail, 2210 m, 8 August 1985, *Atwood 11773 et al.* (BRY); Upper Piute Meadows, 2530 m, 8 August 1985, *Atwood 11704 et al.* (BRY); Nevada County, bog at upper end of mill pond, Marsh Mill about 3.2 km E of Graniteville on Bowman Road, 1768 m, 13 July 1965, *True 2180 & Howell* (CAS); Fall Creek about 8 km N of Yuba Gap, 1707 m, 14 July 1965, *True 2259 & Howell* (CAS); Pierce Meadow, 2.1 km E of Lake Spaulding, 31 July 1997, *Janeway 5296 & Schroder* (CHSC); Plumas County, McRae Meadow, 1981 m, 27 June 1951, *J. T. Howell 27595* (CAS); 0.4 km E of Bucks Summit, 1670 m, 26 June 1981, *J. T. Howell 54384 et al.* (CAS); 1.6 km NE of Little Grass Valley Reservoir, 1646 m, 9 July 2008, *Ahart 15062* (CHSC, WTU); 2.8 air km S of Little Grass Valley Reservoir, 1613 m, 13 August 2008, *Ahart 15183* (CHSC, V, WTU); N side of Pilot Peak, about 14.5 air km NE of La Porte, 2073 m, 20 September 2011, *Ahart 17687* (CHSC); N side Little Grass Valley Reservoir, 2 October 2011, *Janeway & Castro 10756* (CHSC); Butterfly Valley, 1036 m, 17 June 1962, *J. T. Howell 37648* (CAS); Sweetwater Meadow, Butterfly Creek, Butterfly Valley, 1165 m, 2 August 2011, *Zika 25701 et al.* (OSC, WTU); San Bernardino County, E end Bluff Lake, 2256 m, 26 June 1976, *Davidson & Thorne 4446* (NY); Mill Creek Road, grass marsh, 2100 m, 9 July 1931, *Clokey 5243* (GH, RSA); High Meadow Springs SE of Alto Diablo, San Geronio Wilderness, 3078 m, 20 July 1977, *Thorne 49899 et al.* (RSA); Siskiyou County, just below Tom Taylor cabin, 2042 m, 11 August 1968, *Oettinger 486* (RSA, UC); N end Juanita Lake, 1550 m, 16 August 2009, *Zika 24597* (OSC, WTU); Tehama County, Yolla Bolly Mountain Trail, c. 0.8 km W of Cold Fork Trail junction, 2130 m, 14 July 2012, *Zika 25986* (WTU); Route 35, 2.4 air km SE of Rat Trap Gap, Yolla Bolly Mountains, 1665 m, 14 July 2012, *Zika 25983* (WTU); 4 air km WNW of Wilson Lake, 1515 m, 14 July 2008, *Zika 23904* (CHSC, PRA, WTU); Trinity County, E slope South Fork Mountain, 1634 m, 18 June 1992, *Long 2–9* (herbarium of Shasta-Trinity National Forest, Redding); Tulare County, road to Panoramic Point, General Grant Grove, Kings Canyon National Park, 23 July 1948, *Bailey & Bailey 2547* (UC);

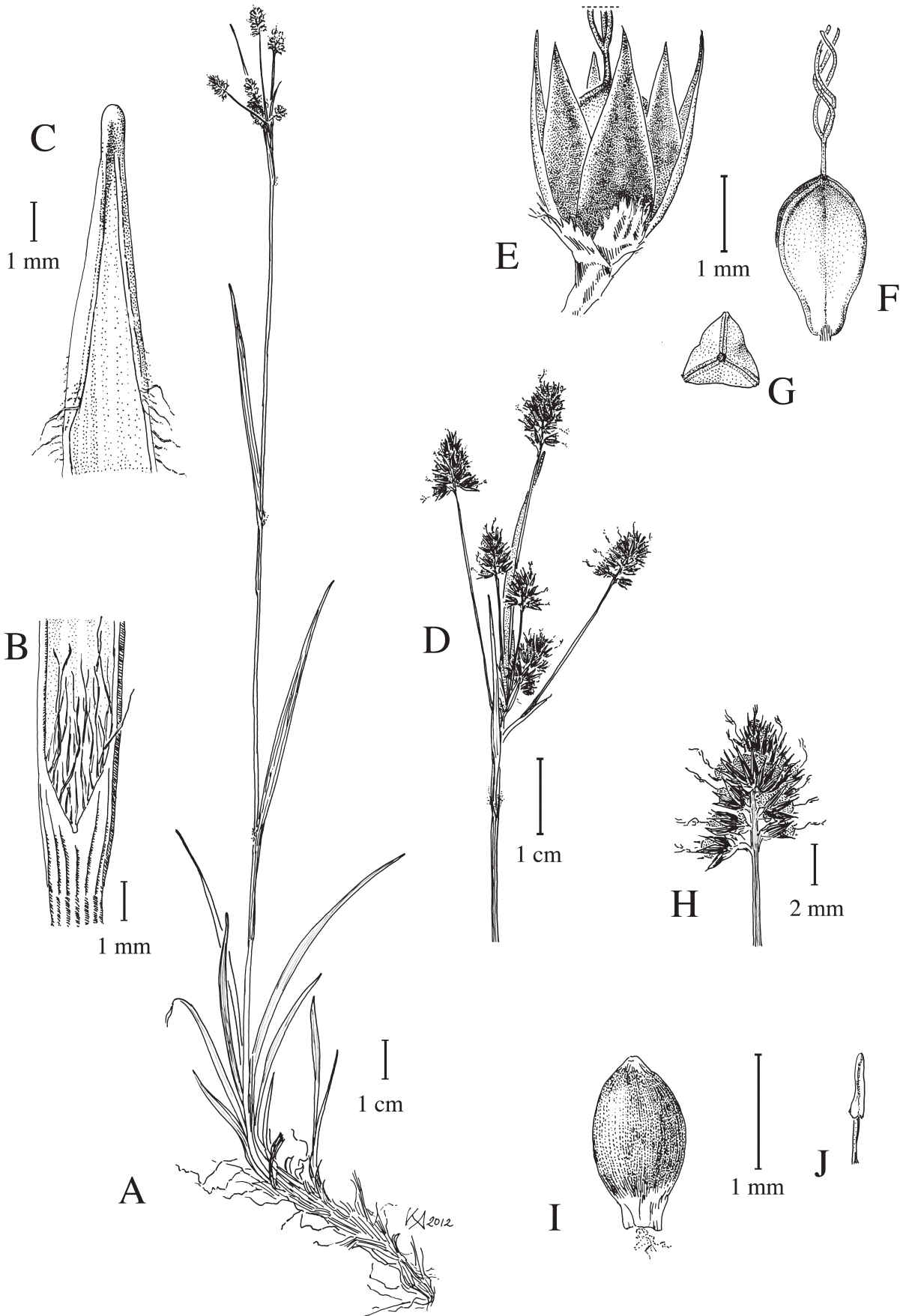


FIGURE 1. *Luzula cascadensis*. A. Habit. B. Stem leaf sheath summit. C. Channeled upper margins and swollen leaf tip. D. Inflorescence. E. Bracteoles and fruiting tepals, partial view of stigmas. F. Stigmas, style and ripe fruit. G. Ripe fruit, top view. H. Spike. I. Seed, basal aril, and hairs. J. Stamen. (A–E, J from the holotype; F–G from *Wilson 16721 & Zika*; I from *Zika 25701 et al.*).



FIGURE 2. Inflorescence variation in *Luzula cascadiensis*, showing congestion or solitary pedunculate heads at one extreme, to umbellate arrangements with short or elongate rays, stiffly erect to spreading-ascending, rarely somewhat arching. A. *Zika* 25624. B. *Zika* 25205. C. *Zika* 25210. D. *Zika* 24592 *et al.* Scale bars 1 cm.

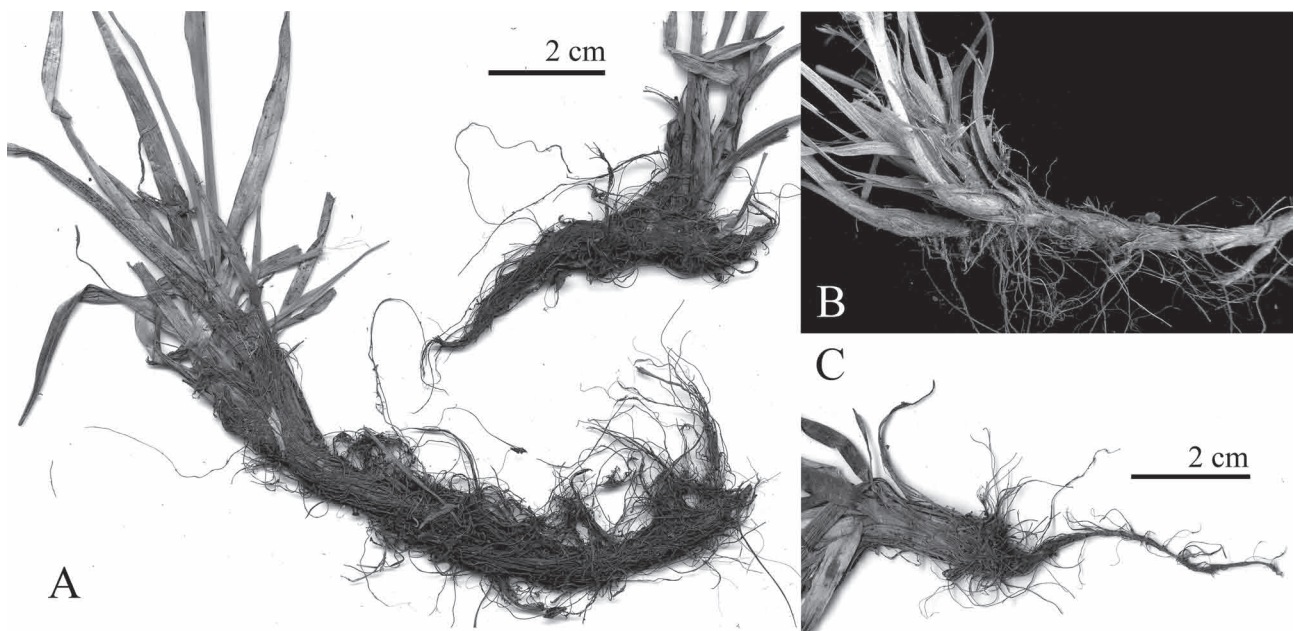


FIGURE 3. Habit, with horizontal rhizomes. A. *Luzula cascadiensis* (*Zika* 25552). B. *Luzula campestris* subsp. *campestris* (*Zika* 24903). C. *Luzula cascadiensis* (*Zika* 25571).

Touhy Creek, Sequoia National Park, 2591 m, 26 July 1950, *Ferris & Lorraine* 12234 (DS, UC); Tobias Meadow, Kern River valley, 10 July 1895, *Dudley* 607 (DS); East Lake, 2926 m, 30 July 1940, *J. T. Howell* 15722 (CAS); South Fork Rock Creek, 3261 m, 9 August 1968, *DeDecker* 1983 (RSA); Horse Meadow, Kern Plateau, 2256 m, 11 July 1966, *Howell* 41753 & *True* (CAS); SW end of Big Meadow just E of Cherry Hill Road, 2377 m, 30 July 1970, *Howell* 47175 & *True* (CAS); W end of Deadwood Meadow, Kern Plateau, 2804 m, 14 July 1971, *Howell* 48459 & *True* (CAS); N end Casa Viejo Meadows, 2530 m, 30 June 1973, *Keefe* 13-505 (CAS); wet meadow near Jug Springs, Golden Trout Wilderness, 1905 m, 16 July 1987, *Tallent* 748 (CAS); Fish Creek just below Loggy Meadow, c. 2300 m, 29 July 2004, *Janeway* 8201 (CHSC); Tuolumne County, meadow SW of Neal Meadow, Yosemite National Park, 2804 m, 18 July 1936, *Hawbecker* 18678 (UC); Yuba County, SE side of Schwartz Meadow, 1219 m, 27 June 1994, *Ahart* 7395 (CHSC); c. 4.8 air km E of Sly Creek Reservoir dam, 1219 m, 27 July 2010, *Ahart* 16914 (CHSC, WTU). **Idaho:**

Custer County, Sawtooth Mountains, c. 400 m NE junction Highway 75 and Stanley Lake Road, 1951 m, 10 July 1996, *Tanaka 112 et al.* (ID); Idaho County, Warren Wagon Road, 0.6 km N of junction to Burgdorf, 1890 m, 27 July 1977, *Davidson 6133* (NY); Clearwater National Forest, Sneakfoot Meadows, 1798 m, 22 July 1987, *Bursik 451* (ID); Vetter Meadows, Moose Meadow Creek Research Natural Area, 1905 m, 28 July 1987, *Bursik 592* (ID); E shore of Big Sand Lake, Bitterroot Mountains, 3 July 1994, *Mancuso 1204* (ID); Valley County, Payette National Forest, Phoebe Meadows proposed Research Natural Area, 1895 m, 21 June 1987, *Bursik 206 et al.* (ID). **Montana:** Ravalli County, Lost Trail Pass, Bitterroot National Forest, 2350 m, 4 August 1988, *Bursik 1499* (ID). **Nevada:** Douglas County, Genoa Peak Road S of Spooner Summit, 2530 m, 13 August 1974, *J. T. Howell 50832 et al.* (CAS); Washoe County, Third Creek, near Mt. Rose, 2591 m, 3 August 1938, *J. T. Howell 14054* (CAS, GH, WTU). **Oregon:** Clackamas County, Clackamas Lake, 23 July 1927, *Peck 15840A* (WILLU); 3.5 air km WNW Barlow Butte, 1110 m, 14 July 2011, *Zika 25624* (WTU); E shore Trillium Lake, 1100 m, 14 July 2011, *Zika 25625* (WTU); Deschutes County, wet grassy ground, Paulina Lake, 2100 m, 29 July 1894, *Leiberg 587* (GH); Soda Creek Trail and meadow, NE Sparks Lake, 1707 m, 15 July 1947, *Ireland 2661.5* (ORE); 1 km E of summit, Charlton Butte, Torrey-Charlton Research Natural Area, Deschutes National Forest, 1701 m, 17 August 1992, *Zika 11869* (WTU); Douglas County, about Diamond Lake, 13 July 1936, *Peck 19285* (WILLU); Grant County, Columbia Hill, 2347 m, 19 July 1937, *Reid 354* (USFS); Mount Ruth, wet meadow, 2438 m, 22 July 1937, *Reid 401* (USFS); Sunflower Spring, Sunflower Flat, Umatilla National Forest, 1265 m, 19 June 2002, *Bradtko 6117* (ID); Lake Creek, Logan Valley, Malheur National Forest, 1579 m, 21 July 2010, *Hinchliff 1068 & Stella* (WS); Morris Mine spring, cirque N side Vinegar Hill, Greenhorn Mountains, 2233 m, 16 August 2011, *Brainerd 1938* (OSC, WTU); headwaters South Fork Desolation Creek, 0.8 km WSW Dupratt Spring, Greenhorn Mountains, 2187 m, 18 August 2011, *Brainerd 1966* (WTU); Harney County, Steens Mountain, 1890 m, 23 July 1954, *Hansen 864* (OSC); Hood River County, Loop Highway, E of Mount Hood, 10 June 1924, *Henderson 777* (GH); Lost Lake, 29 June 1924, *Henderson 778* (GH, ORE); same site, 959 m, 12 August 2000, *Zika 15337* (MICH, OSC, WTU); 1.6 air km SE of Agnes Spring, 1400 m, 10 July 2011, *Zika 25571* (WTU); 2.4 km SW of Elk Mountain, 1335 m, 10 July 2011, *Zika 25567* (WTU); Jackson County, summit Mt. Ashland, 19 July 1913, *Peck 1323* (WILLU); Long John Creek, 1829 m, 25 July 1934, *Wheeler 2976* (CAS, POM); E slope Mt. Ashland, spring near Windsor Chairlift, 2012 m, 8 August 1993, *Rolle 665* (BRY); W summit Mt. Ashland, near Route 20, below Climber's Rocks, Siskiyou Mountains, 2050 m, 22 June 2010, *Zika 25205* (WTU); W of Grouse Gap, 2060 m, 22 July 2010, *Zika 25210* (WTU); 3.5 km SW of Dutchman Peak, 1737 m, 4 July 1988, *Rolle 52* (SOC); 0.3 road km E of Siskiyou Gap, 1815 m, 6 August 1993, *Wilson 6372 et al.* (CHSC); NW end Tamarack Meadow, Siskiyou Mountains, 1810 m, 30 July 2011, *Zika 25665 et al.* (WTU); Josephine County, 2.6 km NE intersection of [road] 3941 on [road] 3897, Siskiyou National Forest, 1469 m, 23 June 1973, *Denton 2568* (ID, OSC); Klamath County, 4.8 km N of Klamath Agency, 10 July 1931, *Peck 16800* (WILLU); West Side Road, 0.8 road km N of Sevenmile Road, 1265 m, 15 August 2009, *Zika 24594* (CHSC, MO, OSC, UC, WTU); Varney Creek, 39 km NE of Klamath Falls, 11 August 1976, *Crosby 901A* (OSC); Vidae Ridge, Crater Lake National Park, 15 August 1950, *Baker 7237* (ID); Sphagnum Bog, Crater Lake National Park, 1610 m, 15 August 1977, *Seyer 83* (SOC); Desolation Swamp, 6.4 km SSE of Lake of the Woods, 1548 m, 10 September 1980, *Christy 2963* (ORE); Lake County, Fremont National Forest, W Teepee Creek, 1665 m, 2 July 2004, *Robohm 04-39 et al.* (WTU); Lane County, Lake Valley, 21 July 1903, *Sheldon S.12569* (ORE); Linn County, Bruno Meadows, Road 2234, Willamette National Forest, 1244 m, 9 July 1994, *Merrifield s.n.* (OSC); Multnomah County, SE end Latourell Prairie, below 20 Road, headwaters North Fork Bull Run River, Mt. Hood, 945 m, 14 August 2009, *Zika 24592 et al.* (PRA, WTU); Umatilla County, Upper Winom Trail, North Fork John Day Wilderness, Umatilla National Forest, 1527 m, 22 June 2002, *Bradtko 6467* (BRY); Wallowa County, Lostine Canyon 32 km above Lostine, 21 July 1933, *Peck 17822* (WILLU); Wasco County, E side Route 26, 3.2 air km SE of Trillium Lake, 1045 m, 16 July 2010, *Zika 25153* (WTU). **Washington:** Skamania County, Barley Meadow, South Prairie, 30 July 1898, *Suksdorf 11595* (WS); Lewis River, Mount Adams, 7 August 1885, *Suksdorf 2515* (WS); Swampy Meadows, 1268 m, 20 September 1988, *Brooks s.n.* (OSC); Yakima County, Woden's Vale, Mount Adams, 12 August 1909, *Suksdorf 6842* (WS).

Etymology:—*Luzula cascadenis*, Cascades woodrush, is named for the volcanic portions of the Cascade Range in Oregon, Washington, and California, where the species is widespread. This taxon has been treated as *Luzula campestris* var. *columbiana*. The epithet *columbiana* could be raised to the species level. We have chosen not to do so because “*cascadenis*” better describes the plant's range and habitat and because *L. campestris* var. *columbiana* was used very little (Kirschner *et al.* 2002, St. John 1936), so its disappearance should not cause much confusion.

Phenology:—The capsules ripen from mid-June through September. Ripe fruits were present on *Zika 25624* on 14 July 2011, as the plant was producing a second flush of flowering shoots.

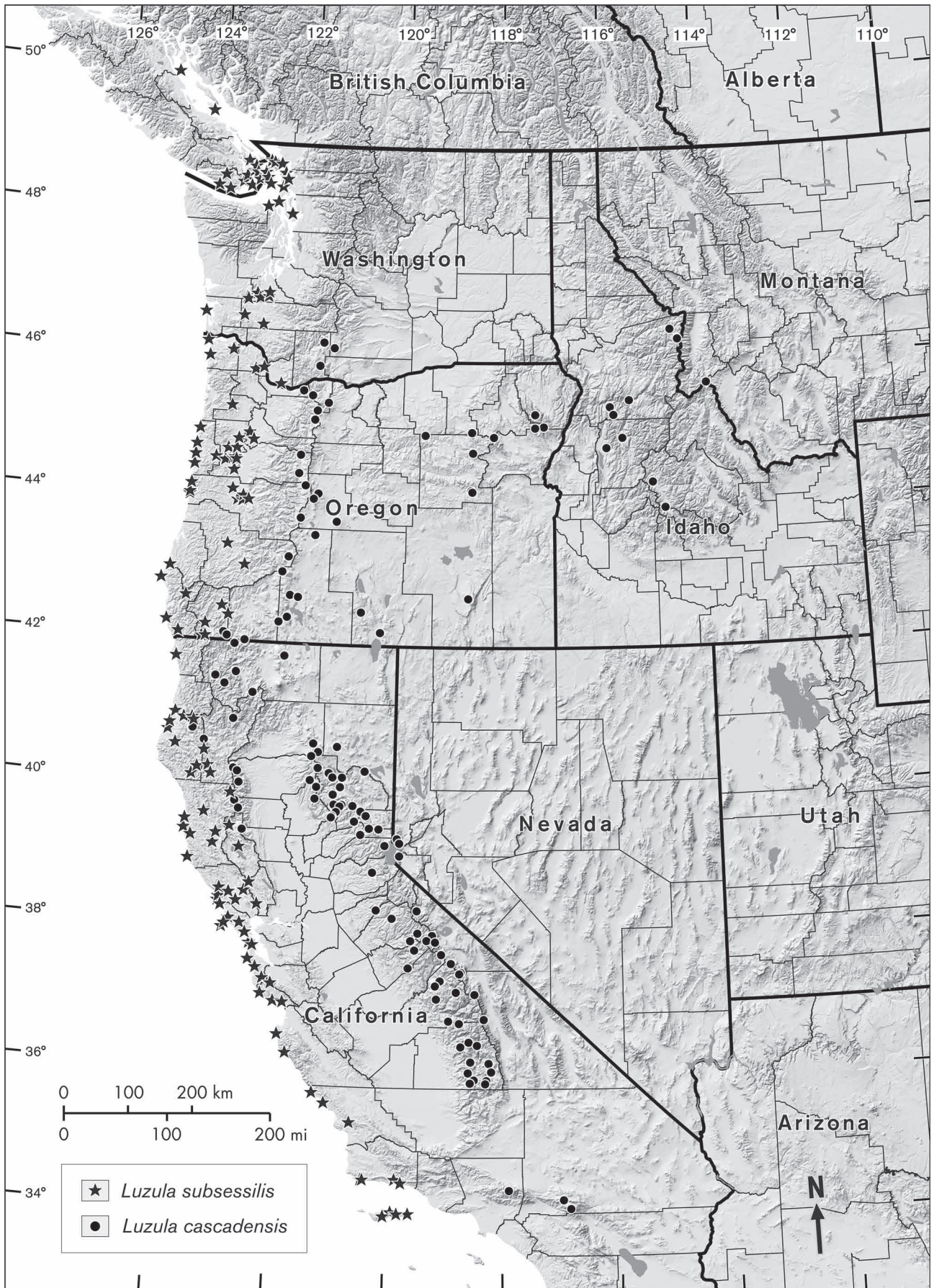


FIGURE 4. Distribution of *Luzula cascadenis* and *L. subsessilis*, plotted from herbarium specimens seen in this study.

Distribution and Ecology:—*Luzula cascadiensis* ranges from Mt. Adams in Washington, east to western Montana, and south to western Nevada and the San Bernardino Mountains of southern California, at elevations of 900–3400 m (Fig. 4). It is found in seasonally to permanently saturated soils, in peatlands, springs, pond shores, wet meadows, and creek banks. The underlying bedrock noted on herbarium labels includes sandstone, schist, peridotite, andesite, diorite, and granodiorite. Common associates are provided in the appendix.

Luzula cascadiensis, like many other members of *Luzula* sect. *Luzula*, has a fleshy pale seed aril that presumably facilitates ant dispersal of the seeds, as has been documented in hundreds of genera (Handel 1978, Bossard 1991, Gibson 1993, Lengyel *et al.* 2010, Gracie 2012).

Notes:—The swollen leaf tips and umbels of spikes place *Luzula cascadiensis* in *Luzula* sect. *Luzula*, as defined in Kirschner *et al.* (2002). Cascade woodrush was confused with *L. campestris* in some recent floristic treatments (*e.g.*, Cronquist 1977; Table 1). Both are long rhizomatous (Fig. 3), but *L. campestris* is a European introduction on disturbed ground at low elevations in western North America (Legler *et al.* 2008), with seeds 1.6–2.1 mm long (including the basal aril), and anthers 1.5–2 mm. *Luzula cascadiensis* is native in montane wetlands, with seeds 1–1.6 mm long, and anthers 0.35–1.2 mm. The rhizomes of *L. campestris* are sturdy structures, and easily extracted when collecting. The rhizomes of *L. cascadiensis* are more fragile and must be extracted with some care in dense wet peat. Many herbarium specimens have broken stubs instead of complete rhizomes. Similar *L. comosa* var. *laxa* lacks horizontal rhizomes, has bulbous-swollen stem bases (Fig. 5), usually has paler tepals, and generally grows in drier soils. The other taxa treated here are usually found in drier soils and produce bulbous shoot bases. In the northeastern part of its range *L. cascadiensis* is sympatric with representatives of the *L. multiflora* complex, and they can have similar umbels of dark dense small spikes. These populations of *Luzula multiflora* are cespitose, lack long rhizomes, and often have wider seeds and longer anthers than *L. cascadiensis*.

Where diploid *Luzula cascadiensis* grows with *L. multiflora* or diploid *L. comosa* var. *laxa*, they occupy slightly different positions on the gradient of soil moisture. Morphologically intermediate plants that might be hybrids appear to be extremely rare. Hybridization with the presumed polyploid *L. multiflora* would not be expected (Kirschner 1991). However, greenhouse hybrids of *L. cascadiensis* with the Asian diploid *L. lutescens* (Koidzumi in Matsumura 1912: 105, fig. 53) Kirschner & Miyamoto (in Kirschner & Kaplan 2001: 1110) were produced and were partly fertile (Nordenskiöld 1956). This, and the work of Kirschner (1991, 1992b) suggests hybridization between *L. cascadiensis* and *L. comosa* var. *laxa* may be a possible explanation for a few plants that display intermediate morphological characters and grow in transitional habitats near the two putative parents.

2. ***Luzula comosa*** Meyer (1823: 21). (Figs. 5A–B, 6, 7A). *Luzula campestris* (Linnaeus 1753: 329) de Candolle (1805: 161) var. *comosa* (Meyer 1823: 21) Fernald & Wiegand (1913: 41). *Juncooides campestris* (Linnaeus 1753: 329) Kuntze (1891: 724) var. *comosa* (Meyer 1823: 21) Kuntze (1891: 724). *Juncooides comosa* (Meyer 1823: 21) Sheldon (1894: 64). *Luzula multiflora* (Ehrhart 1790: 14) Lejeune (1811: 169) subsp. *comosa* (Meyer 1823: 21) Hultén (1943: 437). *Luzula multiflora* (Ehrhart 1790: 14) Lejeune (1811: 169) var. *comosa* (Meyer 1823: 21) St. John (1960: 96).

Type:—[CANADA. British Columbia: Vancouver Island, Nootka Sound, Friendly Cove], Sinus Nutkaensis, [mid-August 1791], *T. P. X. Haenke s.n.* (holotype PR).

Perennial herb, tufted, lacking elongate horizontal rhizomes; stem 10–78 cm tall, usually exceeding the leaves, with age usually bulbous thickened basally; basal sheaths pale brown, sometimes pink or purple-striped. Leaves 2–5, distributed on the proximal $\frac{3}{4}$ of the stems; blades herbaceous, 60–330 × 1.5–7.5 mm, flat, becoming channeled near swollen, blunt, pale or brownish apex, margins spreading hairy, at least proximally, the margins (at 16 ×) papillose serrate; leaf sheaths tight or loose, densely long white hairy at V-shaped apex. Vegetative rosettes with blades to 360 × 2–7 mm. **Inflorescences** 1–11 × 0.5–4.5 cm, congested into a single or lobed head or open with (1)2–8(17) spikes. Inflorescence or its spikes each subtended by a bract, this green or reddish, shorter than to longer than the inflorescence, apices swollen, blunt, and discolored, apex acute to acuminate. Bracteoles subtending individual flowers three, scarious, acuminate to acute, margins erose or hairy, becoming increasingly dissected with age. **Tepals** 6, (2)2.2–3.9(4.2) mm, scarious, pale brown or mid brown, rarely dark brown, stamens 6, filaments 0.4–0.7 mm, anthers yellow, linear, 0.5–0.9(1.1) mm, styles straight, persisting, easily broken, (0.2)0.4–0.9(1.1) mm. **Capsules** obovate trigonous, 0.6–2.7 × 1.2–1.9 mm, apices acute or blunt, occasionally truncate, with three seeds (1.1)1.2–2.1 mm long (including basal aril) × 0.6–1.1(1.2) mm, fleshy aril pale, 0.15–0.6(0.7) mm long, not including the fibrillose base.

Phenology:—The capsules ripen from May through August.

Luzula comosa is represented by two largely allopatric varieties, described below.

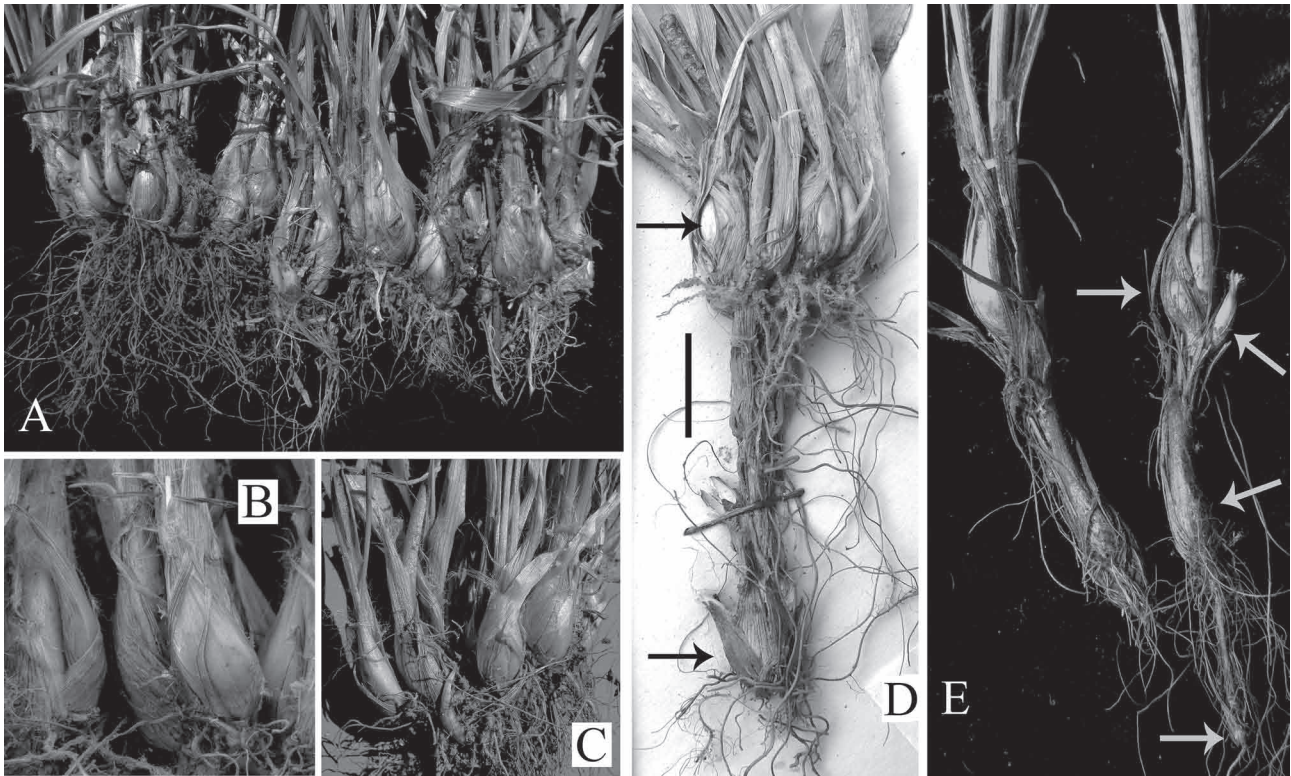


FIGURE 5. Bulb-based habit. A–B. *Luzula comosa* var. *laxa* (Zika 24456). C. *Luzula macrantha* (Zika 25869 & Janeway). D–E. Unusual forms showing bulbs (indicated by arrows) and vertical rhizomes. D. *Luzula macrantha* (Wolf 1167 RSA). Scale bar 1 cm. E. *Luzula subsessilis* (Zika 24801).

2A. *Luzula comosa* Meyer (1823: 21) var. *comosa* (Fig. 6A).

Stems 14–78 cm tall. Leaves (2)3–5, 6–33 cm; leaf sheaths tight or slightly loose. Vegetative rosettes with blades to 360×3.5 –6 mm. **Inflorescences** 1.3–3 \times 1–2.1 cm, congested into a single or lobed head of 4–10 dense spikes (rarely with a short branch and spike elevated above terminal cluster), occasionally with remote, long-peduncled spike from axil of distal cauline leaf. Axis of spikes subtended by inconspicuous bracts shorter or longer than the spike. **Tepals** 2.3–3.5(4) mm. Filaments 0.5–0.7 mm. Styles (0.2)0.4–0.8 mm. **Capsules** 1.6–2.4 \times 1.2–1.5 mm, apices occasionally truncate. Seeds (1.1)1.2–1.6(1.85) mm long (including basal aril) \times 0.6–0.9 mm, aril 0.15–0.6 mm long.

Most specimens of *Luzula comosa* var. *comosa* are tetraploids with $2n = 24$ and unfragmented chromosomes (Nordenskiöld 1951). We report here for the first time a diploid voucher from Vancouver Island, British Columbia, with $2n = 12$, Nordenskiöld 50-11 (UPS).

Additional specimens examined:—CANADA. **British Columbia:** Queen Charlotte Is. Graham Is., W outskirts Queen Charlotte City, 13 July 1957, *Calder 22480 et al.* (GH [chromosome voucher $2n = 24$]); Graham Is., near Sue Lake, 21 June 1983, *Ryan 83-017* (OSC); Moresby Is., between Skidegate and Skidegate Mission, 11 June 1957, *Calder 21398 et al.* (UBC [chromosome voucher $2n = 24$]); Moresby Is. E coast, East Copper Is. in Skincuttle Inlet, 7 July 1957, *Calder 22257 et al.* (UBC [chromosome voucher $2n = 24$]); Moresby Is. E coast, Limestone Is. off Louise Is., 10 July 1957, *Calder 22415 et al.* (RSA [chromosome voucher $2n = 24$]); Moresby Is., 2.4 km NE of Alliford Bay, 27 June 1957, *Calder 21850 et al.* (DS, OSC, WS [chromosome voucher $2n = 24$]); Port Edward, 11.3 km S of Prince Rupert, 18 July 1954, *Calder 13160 et al.* (WS); Vancouver Is., Parksville, 3 June 1949, Nordenskiöld 50-20 (UPS [2 chromosome vouchers, both $2n = 24$]); Port Alberni, 2 June 1949, Nordenskiöld 50-11 (UPS [chromosome voucher, $2n = 12$]); S shore Jakobson Point, Brooks Peninsula, 11 August 1984, *Ogilvie et al. 8481111* (V); near First Nanaimo Lake, 21 June 1950, *Krajina 4549 et al.* (UBC); North Nanaimo River, 270 m, 22 June 1950, *Krajina 5115 et al.* (UBC); near Ucluelet, 17 June 1917, *Dittenry 1128* (RM); Campbell River, NW of airport, 150 m, 18–21 May 1987, *Češka 21326 & Klinka* (UBC); Kyuquot, Kaouk River, 0 m, 3 July 1958, *T. M. C. Taylor & Szczawinski 304* (UBC); Read Is., Flower Is. off Burdwood Bay, 5 m, *Češka 19358 & Češka* (UBC); Capilano Flats, N of Lions Gate Bridge, 20 May 1947, *Jeffery 117* (UBC); Chilliwack Valley, 7 July 1901, *Macoun 34672* (CU, GH).

UNITED STATES. **Alaska:** shores of Behm Canal, 4 July 1892, *T. Howell s.n.* (ORE); Revilla Gigedo Is., 14 August 1895, *T. Howell 1675* (DS, ORE [2 sheets]). **California:** Humboldt County, Eureka, 30 April 1899, *Tracy 291* (WTU); Marin County, Potrero Meadow, Mt. Tamalpais, 7 July 1946, *J. T. Howell 22201* (CAS, RM, WS); Sonoma County, E side Bodega Head, 2 m, 26 June 2012, *Zika 25942B* (WTU); Pitkin Marsh, near Forestville, W branch Upper Marsh, 7 June 1951, *Rubtzoff 131* (CAS, DS). **Oregon:** Clatsop County, Cannon Beach, 1 July 1924, *Peck 13298* (WILLU); near Nestucca Bay, 19 August 1909, *Peck 1332* (WILLU); Seaside, 10 July 1947, *Peck 24277* (WILLU); Columbia County, St. Helens, 28 May 1895, *Suksdorf 2515* (WS); Coos County, mixed coll. with *L. subsessilis*, Golden and Silver Falls State Park, 9 August 1988, *R. L. Thompson 88-1816 et al.* (ORE, SOC); Life Saving Station, Coos Bay, 29 May 1931, *Henderson 13781* (ORE); Curry County, 4.8 km S of Port Orford, 1 July 1919, *Peck 8616* (BH, GH, WILLU); Pyramid Rock, 1 July 1934, *Leach 4778* (ORE); Lane County, Siltcoos Lake, 13 June 1934, *Andrews s.n.* (ORE); Lincoln County, near Newport, 9 June 1943, *Gilkey s.n.* (OSC). **Washington:** Lewis County, [railroad], 28 April 1934, *Otis 1858* (WS); Skagit County, 4.8 km W of Rockport, 61 m, 26 May 1972, *Naas & Cheney 1351* (USFS); Thurston County, near Mud Bay, 0 m, 9 June 1933, *Otis s.n.* (WS); [railroad] grade, S of Tumwater, 3 May 1934, *Otis 1880* (WS).

Distribution and Ecology:—*Luzula comosa* var. *comosa*, pale woodrush, is often a littoral plant, ranging from the central California coast north to southeastern Alaska. Most collections are from less than 200 m elevation, on sandy or gravelly sea beaches, cliffs, fjords, shores, and maritime forests. Common associates are provided in the appendix.



FIGURE 6. Inflorescence variation in *Luzula comosa*. A. *Luzula comosa* var. *comosa*, dense clusters (*Zika 25942B*). B. *Luzula comosa* var. *laxa*, typical umbellate inflorescences with loosely flowered individual spikes on erect or ascending rays (*Wilson 16720 & Zika*). C. *Luzula comosa* var. *laxa*, showing variation in inflorescence density; most plants with elongate rays (*Zika 25293 et al.*). D. *Luzula comosa* var. *laxa*, unusual compound umbels, left and center (*Zika 25530*).

Notes:—A dense terminal inflorescence is characteristic of *Luzula comosa* var. *comosa* (Fig. 6A). Occasional stems show a long-peduncled spike from the distal leaf axil. The inflorescence is the primary means to distinguish it from *L. comosa* var. *laxa*, which has a branching, umbellate inflorescence (Figs. 6B, D). Transitional forms are found infrequently, away from the coast, such as *Zika 25293 et al.* (Fig. 6C). The pale tepals help separate *L. comosa* var. *comosa* from *L. subsessilis*, which has a dense terminal inflorescence but black tepals (Table 2). Rarely *L. comosa* var. *comosa* can have darker tepals, mid-brown or even darker, for example in Sonoma County. These darker plants are separable from *L. subsessilis* in the area by their lack of axillary peduncled spikes, somewhat less densely hairy and shorter-hairy bracteoles, and their preference for more hydric soils. They mature in summer, whereas nearby colonies of *L. subsessilis* mature in spring. Occasional forms of *L. cascadiensis* have congested inflorescences and pale tepals, but they are rhizomatous and grow further inland, at higher elevations than *L. comosa* var. *comosa*.

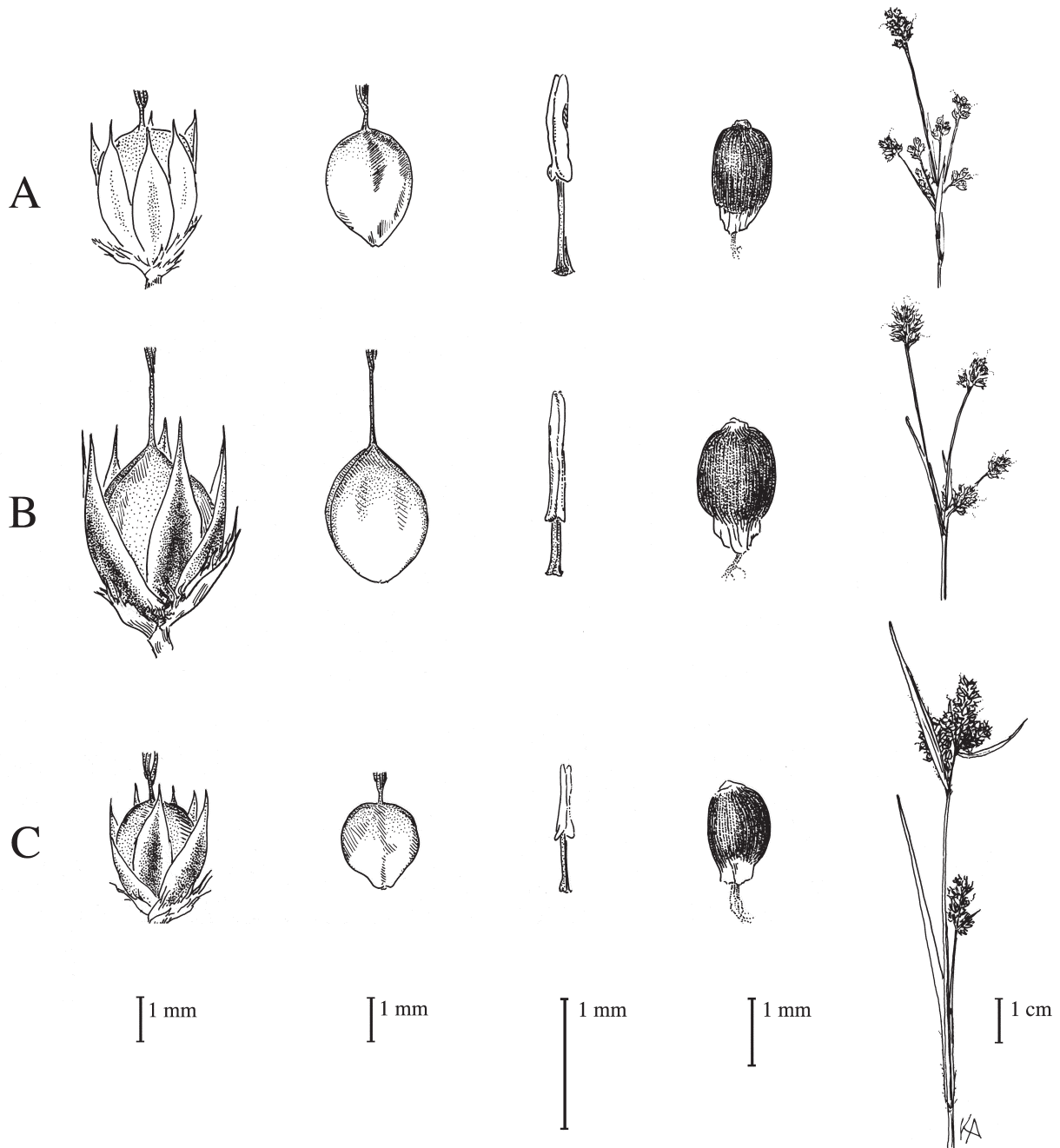


FIGURE 7. Comparisons of three *Luzula* with bulbous bases, by columns from left to right: bracteoles and fruiting tepals, stigmas truncated; stigmas, styles, and ripe fruits; stamens; seeds; inflorescences. A. *Luzula comosa* var. *laxa* (*Zika 24889*, except stamen (*Zika 25024*) and inflorescence (*Wilson 16720 & Zika*). B. *Luzula macrantha* (*Zika 24810 & Lang*). C. *Luzula subsessilis* (*Zika 18435*, except stamen and seed, *Zika 25892 & Brainerd*).

2B. *Luzula comosa* Meyer (1823: 21) var. *laxa* Buchenau (1906: 83). (Figs. 5A, 6B–D, 7A).

Type:—UNITED STATES. Idaho: [Benewah County], Coeur d'Alene Mountains, along St. Mary's River, open ponderosa forests, 990 m, 26 [or 27] June 1895, *J. B. Leiberger s.n.* [= *Leiberger 1083*] (lectotype, here designated, US, isolectotype ORE).

Stems 10–39(50) cm tall. Leaves 2–4, 6–16 cm; leaf sheaths tight or loose. Vegetative rosettes with blades to 225 × 2–7 mm. **Inflorescences** (1)2–11 × 0.5–4.5 cm, open umbels of (1)2–8(17) spikes (rarely compound or congested in a terminal cluster, but then the population with numerous ordinary umbels on other plants). The rays 1–7.5 cm, stiffly erect to spreading ascending (divaricate), spikes 5–17 × 5–8.5 mm, 4–22 flowered, loose (dense) basally. Inflorescence rays subtended by inconspicuous bracts, often fimbriate, shorter than the ray. **Tepals** (2)2.2–3.9(4.2) mm, usually scarious or pale brown. Filaments 0.4–0.7 mm. Styles 0.2–0.9(1.1) mm. Capsules 1.9–2.7 × 1.2–1.9 mm. Seeds (1.1)1.2–2.1 mm long (including basal aril) × (0.6)0.65–1.1(1.2) mm, aril (0.2)0.3–0.6(0.7) mm long.

Chromosome numbers of *Luzula comosa* var. *laxa* were reported as diploid $2n = 12$ (Nordenskiöld 1951), and a number of herbarium vouchers confirm this. However, chromosome vouchers of *L. comosa* var. *laxa* from Mariposa and Tuolumne counties, California, had $2n = 24$. Originally identified as *L. comosa* var. *comosa* (Nordenskiöld 1951), the vouchers were re-identified as *L. comosa* var. *laxa* in the course of this study, and they constitute the first reports of tetraploid *L. comosa* var. *laxa*.

Additional specimens examined:—CANADA. **Alberta:** bog in Scotford Sandhills, 6.4 km E and 6.4 km N of Fort Saskatchewan, 21 June 1945, *Turner 4410* (UBC); river flat, 9.7 km NE of Fort Saskatchewan, 28 June 1942, *Turner 2970* (ORE); Notikewin, 21 July 1941, *Moss 6183* (GH). **British Columbia:** Alaska Highway, SE of Pink Mountain at Mile 122, 945 m, 16 July 1960, *Calder 27078 & Kukkonen* (UBC); Castlegar, 400 m, 23 June 1962, *T. M. C. Taylor & Szczawinski 633* (UBC); between Gray Creek and Crawford Bay, [Kootenay Lake], 15 May 1947, *McCalla 9446* (UBC); Carmi Creek, Dam # 1, Okanagan Falls road, 1 August 1991, *Češka 27494* (V); NW slope Mt. Ida, 8 km SW of Salmon Arm, 4 June 1953, *Calder 8674 & Savile* (UBC); Sproat, Columbia River, 24 June 1890, *Macoun s.n.* (CAS); Ecological Preserve # 89, Skagit River Cottonwoods, Hope, 26 July 1988, *Oglivie & Češka 24500* (V); [seed from] Harrison Springs, Agassiz, [cultivated in Ultuna], 17 April 1950, *Nordenskiöld L3A3Ca8* (UPS [chromosome voucher $2n = 12$]); Vancouver Is., Elk Lake, 4 May 1914, *Macoun 609* (V); Port Alberni, 2 June 1949, *Nordenskiöld 50-10* (UPS [chromosome voucher, $2n = 12$]); Wreck Bay near Ucluelet, 9 m, 9 June 1957, *Szczawinski 5738* (UBC); Goldstream, 18 May 1956, *Melburn s.n.* (V); Coquitlam, 14 May 1997, *Lomer 97-40* (UBC); Pitt Meadows, 30 May 1973, *Brink 36* (UBC). **Saskatchewan:** Cypress Hills Park, 1219 m, 10 July 1947, *Breitung 4580* (RM).

UNITED STATES. **Arizona:** Rucker Valley and Apache Pass, 1881, *Lemmon 311472* (GH); Webber's Cabin, Santa Catalina Mountains, 2316 m, 27 June 1917, *Shreve 5283* (GH, OSC); Coconino County, East Miller Canyon, 2286 m, 24 July 1987, *Boucher 589* (ASC); Graham County, Snow Flat, Pinaleno Mountains, 2730 m, 2 August 2011, *Licher 3182* (ASC, WTU). **California:** Alpine County, between Pacific and Hermit valleys on Ebbetts Pass road, 2134 m, 27 June 1978, *J. T. Howell 53095 et al.* (CAS); Butte County, 0.8 km SW of Bald Mountain, 1615 m, 2 July 1986, *Ahart 5341* (CHSC); Lassen Forest, Colby Meadows, 1281 m, 4 July 1929, *Robinson 123* (USFS); Mooreville Ridge Road, 1025 m, 6 July 2011, *Zika 25530* (CAS, WTU); Calaveras County, Calaveras Big Trees, August 1906, *Dudley s.n.* (DS); Del Norte County, 6.4 air km ESE of Oregon Mountain, 530 m, 21 June 2010, *Zika 24940* (CHSC, JEPS, OSC, WTU); El Dorado County, near foot Echo Summit grade, 1.6 km SW of Meyers, 2012 m, 9 July 1963, *J. T. Howell 39662* (CAS); Fresno County, 1.7 km E Dogtooth Peak, Helms Creek tributary, 2575 m, 14 July 1996, *York 1223* (CAS); Glenn County, Plaskett Meadows, 1829 m, 3 August 1943, *J. T. Howell 18983* (CAS); Humboldt County, serpentine savannah, 1 air km SSW Horse Mountain, 1310 m, 3 July 2011, *Zika 25494B* (WTU); Kern County, Kern Plateau, Pine Flat, 2163 m, 13 July 1971, *J. T. Howell 48351 & True* (CAS); Lassen County, NW end Clover Valley, Susan River basin, 14 July 2008, *Zika 23895* (CHSC, NY, OSC, PRA, WS, WTU); Los Angeles County, Charlton Flats burn (of 1954), 1600 m, 2 July 1969, *Thorne 38231* (CAS); Mariposa County, [seed from] Bear Creek, [cultivated in Ultuna], 22 June 1950, *Nordenskiöld 50-17* (UPS [chromosome voucher $2n = 24$]); Yosemite National Park, along Foresta Creek, Foresta, 25 June 1959, *Smith 1575* (CAS); Mendocino County, W side Ten Mile Road, 0.8 road km S of Schooner Gulch Road, 310 m, 21 June 2010, *Zika 24969* (WTU); Nevada County, 0.5 km W Soda Springs town, 2040 m, 17 July 2008, *Zika 23915 & Wetherwax* (CHSC, WTU); Placer County, Cisco, Camp Yuba, 6 July 1870, *Kellogg s.n.* (CAS); Plumas County, 3.2 km N of Ohio Ravine, 1700 m, 30 July 1982, *Ahart 3736* (CAS, CHSC, MO, OSC); S edge Little Willow Lake, 1831 m, 19 July 2003, *Janeway 7908* (CHSC); Riverside County, Idyllwild, San Jacinto Mountains, 1615 m, 19 July 1919, *Spencer 1197* (BH, CAS); San Bernardino County, S and E shores Bluff Lake, 2315 m, San Bernardino Mountains, 5 August 2010, *Zika 25276 & Otting* (OSC, WTU); South Fork Meadows, South Fork Santa Ana River, 2500 m, San Geronio Wilderness Area, 5 August 2010, *Zika 25293 et al.* (JEPS, OSC,

PRA, RSA, WTU); Sierra County, W end Church Meadows, 2030 m, 24 July 1998, *Janeway 5830* (CHSC); Siskiyou County, moist flat, Road 26, 1905 m, 8 August 2010, *Wilson 16273 & Brainerd* (WTU); Canyon Creek, Marble Mountains, 914 m, 11 June 1962, *Breedlove 3347* (DS); Shasta Springs, 27 May 1923, *Eastwood 11956A* (CAS); Tehama County, road to Dry Lake, 0.2 km W of Highway 89, 1895 m, 1 August 2011, *Wilson 16720 & Zika* (WTU); Trinity County, 9.7 km SW of Trinity Center on road to Weaverville, 884 m, 20 May 1980, *J. T. Howell 53496 et al.* (CAS); Tuolumne County, Elizabeth Lake meadow, 2987 m, 15 August 1916, *Smiley 792* (GH); [seed from] Big Creek, [cultivated in Ultuna], 22 June 1950, *Nordenskiöld 50-19* (UPS [chromosome voucher $2n = 24$]); Miguel Meadow, W Hetch Hetchy, Yosemite National Park, 1585 m, 7 July 1938, *Mason 11862* (UC); [seed from] Hetch Hetchy, 1189 m, [cultivated in Ultuna], 4 May 1950, 4 June 1950, and 22 June 1950, *Nordenskiöld 50-16* (UPS [3 chromosome vouchers, all $2n = 24$]); above Hog Ranch Cabin, Mather, 1400 m, 25 July 1937, *J. Clausen 1535* (UC); [seed from] Mather, 1400 m, [cultivated in Ultuna], 22 June 1950, *Nordenskiöld 50-13* (UPS [chromosome voucher $2n = 24$]); Yuba County, 5.8 km NE of Strawberry Valley on LaPorte-Quincy road, 1280 m, 22 June 1981, *J. T. Howell 54090 et al.* (CAS).

Colorado: El Paso County, Seven Bridges Trail, off Gold Camp Road, 0.8 km from Jones Park, 2682 m, 22 June 2006, *Brouwer 6.231* (COLO); Crystal Park, 2600 m, 8 July 1901, *Clements & Clements 321* (DS, GH, MO, RM). **Idaho:** Bonner County, NE shore Hope Point, Ellisport Bay, Pend Oreille Lake, 640 m, 24 July 2012, *Zika 25994* (WTU); Idaho County, Taylor Gulch, just S Scott Saddle, burned by wildfire August 1992, 26 May 1994, *Sondenaa 17* (ID); Kootenai County, N shore Lake Coeur d'Alene, 19 May 1935, *Hitchcock 2622 & Samuel* (ORE, OSC, POM, RM, WS); Latah County, Flannigan Creek, Viola-Potlach Road, Viola Mountains, 19 July 1919, *Ferris 1322 & Duthie* (DS); S ridge Moscow Mountain, 22 May 1954, *Baker 11438* (WTU); Nez Perce County, 3.2 km W of Lenore, 4 May 1946, *Daubenmire 46128* (WS); Shoshone County, trail along Willow Creek to Stevens Lake, 1451 m, 26 June 2007, *Brunsfeld 5826 et al.* (ID); Valley County, Salmon River Range, Lick Creek confluence with Secesh River, 1311 m, 7 July 1990, *Henderson 7766* (ID). **Montana:** Flathead County, Columbia Falls, 15 June 1892, *Williams s.n.* (GH); Route 2, Marias Pass, 1595 m, 25 July 2012, *Zika 26004* (WTU); Granite County, Harrys Flat Camp, Rock Creek Canyon, 6 July 1946, *Hitchcock 14385 & Muhlick* (WS, WTU); Mineral County, Lee Creek Camp, Lolo Hot Springs, 12 July 1946, *Hitchcock 14612 & Muhlick* (WS, WTU); Missoula County, Swan River Valley, W Holland Lake, 3 July 1955, *Cronquist 7874* (GH, RSA, WS, WTU); Ravalli County, Bass Lake Trail about 8 km W of Bass Creek Campground, 9 July 1966, *Woodland 396 & Woodland* (WS); Sanders County, near head of trail along North Fork Bull River, 853 m, 20 June 1985, *Clampitt 174* (WTU). **Nevada:** Washoe County, George Whittell Forest and Wildlife Area, Little Valley, W of Franktown, 2055 m, 27 June 1973, *J. T. Howell 49334 et al.* (CAS). **New Mexico:** Sandoval County, Valles Caldera National Preserve, Rito de los Indios Canyon, where Cabin Creek joins Indios Creek, 2758 m, 14 June 2001, *Jacobs 21* (COLO). **Oregon:** Benton County, Marys Peak Recreation Area, N Conner Camp on East Ridge Trail, 16 June 2009, *Wilson 15592* (OSC); Clackamas County, E shore Little Crater Lake, 990 m, 8 July 2011, *Zika 25551* (WTU); Coos County, Golden and Silver Bells State Park, 29 June 1988, *R. L. Thompson 88-1128 & Skeese* (SOC); Crook County, Big Meadows, Deschutes River, 1370 m, 26 July 1894, *Leiberg 525* (GH, ORE); Curry County, Waterman's on the Winchuck River, 7 May 1929, *Henderson 10093* (ORE); Douglas County, near Bushnell Rocks, 510 m, 7 June 2008, *Wilson 14565* (OSC); NE shore Diamond Lake, 1580 m, 21 July 2010, *Zika 25191* (WTU); Grant County, dry slope, mountain above Strawberry Lake, 15 July 1921, *Peck 10228* (WILLU); Hood River County, Lookout Mountain, 4 September 1938, *Peck 20137* (WILLU); Jackson County, between Logan Drive and Ditch Road, Ashland, 713 m, 15 May 2010, *Zika 24809 & Lang* (CHSC, RSA, WTU); Josephine County, near corner Monument Drive and Camp Jay Road, 360 m, 14 May 2011, *Zika 25849* (WTU); Klamath County, Four-Mile Lake, 2 July 1931, *Peck 16594A* (WILLU); Lake County, Dairy Creek, near Lakeview, 4 July 1927, *Peck 15454* (WILLU); Lane County, Walton, 10 July 1915, *J. C. Nelson 319* (DS); summit Scott Mountain, 1867 m, 18 July 1945, *Ireland 2132* (ORE); Linn County, Carpenter Saddle, 1372 m, 19 July 1964, *Franklin 429* (OSC, USFS); Marion County, Salem, May 1911, *Peck 1327* (WILLU); Morrow County, Blue Mountains, W side Lake Penland, 1524 m, 25 July 2008, *Brainerd 1264 & Otting* (ID, OSC); Multnomah County, mountain above Bridal Veil, 25 June 1911, *Peck 1329* (WILLU); Tillamook County, Tillamook Burn area, 4.8 km SE of Blue Lake, 1006 m, 1 July 1975, *Chambers 4145* (OSC); Union County, Starkey Range, 1463 m, 23 June 1941, *Keil 1096* (USFS); Wallowa County, Imnaha River Road, 1219 m, 10 June 1963, *Mason 6008* (OSC). **South Dakota:** Custer County, Black Hills, Black Elk Wilderness, trail SW of Mt. Rushmore near Grizzly Creek, 1597 m, 21 June 2001, *Mayer 239* (RM); Lawrence County, Deadwood Gulch, 1 July 1928, *Over 17577* (RM); Pennington County, Horse Creek, 1372 m, 28 June 1957, *Pase 840* (USFS). **Utah:** Summit County, Stillwater Fork, Uintah Mountains, 2682 m, 15 July 1926, *Payson & Payson 4971* (DS, POM). **Washington:** Clallam County, Elwha River, 1.6 km S of Little River bridge, 60 m, 3 July 2003, *Tisch 4199* (herbarium of Olympic National Park, Port Angeles); Clark County, Barberton, 70 m, 24 May 2010, *Zika 24866* (CHSC, OSC, WS, WTU); Columbia County, Blue Mountains, 10 June 1897, *Horner B503* (GH); Ferry County, near Trout Lake, Hoodoo Canyon, 1000 m,

2 June 2000, *Zika 15059* (WTU); [Grays Harbor County], near Quinault, June-July 1902, *Conard 413* (GH); Jefferson County, near Old Fort Townsend State Park, Quimper Peninsula, 75 m, 23 June 2009, *Zika 24560* & *Weinmann* (OSC, PRA, WTU); King County, University of Washington hospital shrub bed, Seattle, 11 May 1990, *Johnson 445* (WTUH);

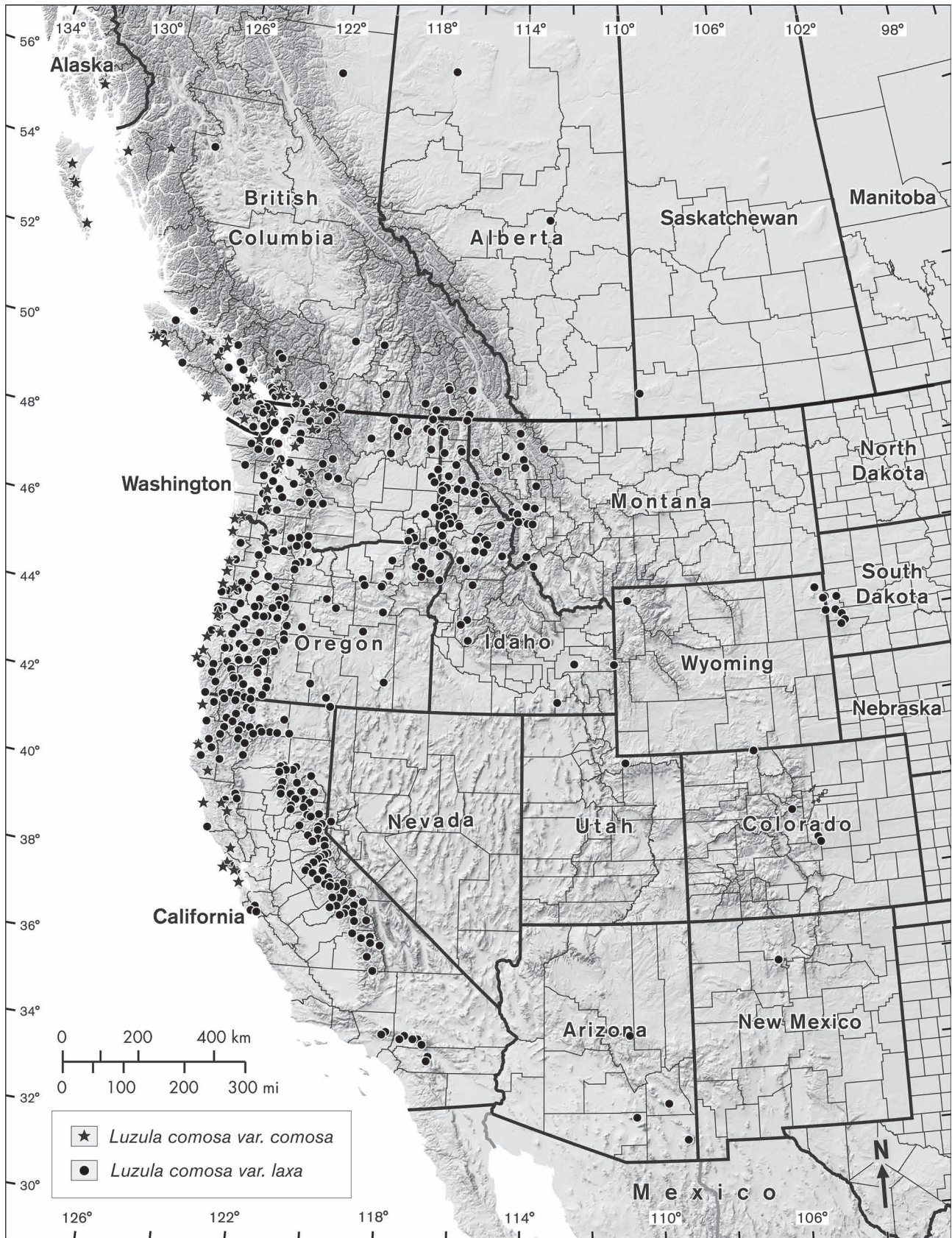


FIGURE 8. Distribution of *Luzula comosa* var. *comosa* and var. *laxa*, plotted from herbarium specimens seen in this study.

Klickitat County, a few miles NE of Bingen, Hog Prairie, 9 July 1926, *Suksdorf 12039* (WS); Lewis County, Wildwood Road, Black Creek drainage, 6 air km NW of Ryderwood, 120 m, 24 May 2010, *Zika 24870* (MO, WTU); Drews Prairie, 90 m, 1 June 2010, *Zika 24889* (CHSC, OSC, WTU); Pend Oreille County, near Tiger Slough, 620 m, 27 June 2010, *Zika 25024* (WTU); Pierce County, Longmire, Mt. Rainier, 10 July 1937, *Jones 9885* (BH, GH); San Juan County, E shore McConnell Is., 30 May 2006, *Giblin 476* (WTU); Skagit County, Vendovi Is., 1 June 2011, *Dunwiddie 2011–54* (WTU); Skamania County, Ice Cave, 22 July 1894, *Suksdorf 2511* (DS, ID, ORE, OSC, WS); Spokane County, Hangman Creek, 460 m, 16 May 1893, *Sandberg & Leiberger 19* (GH, ORE, S, UPS, US); Newman Lake, 27 May 1938, *Stillinger 432* (ID); Stevens County, Little Pend Oreille National Wildlife Refuge, Little Pend Oreille River, 10 air mi SE Colville, 701 m, 23 May 1995, *Wood 285* (WTU); Thurston County, near Mima Mounds Natural Area, 60 m, 3 June 2009, *Zika 24456* (PRA, WS, WTU); Walla Walla County, Lewis Ridge Road, 1189 m, 30 June 1982, *Grable 8958* (WS); Yakima County, base Devils Table, Little Rattlesnake Creek canyon, 949 m, 5 July 2007, *Jensen 190 et al.* (WTU). **Wyoming:** Carbon County, Sierra Madre, 6.4 air km SSW of Blackhall Mountain, Encampment River, 2576 m, 28 July 1988, *Kastning 803 et al.* (RM); Crook County, Black Hills, Geis Springs, 8 air km E of Alva, 1433 m, 13 July 1983, *Hartman 16086* (RM); Park County, 1960 fire scar, Central Plateau, Yellowstone Park, 2499 m, 13 August 1966, *Taylor 66–117* (RM); Weston County, Black Hills, W Mallo Camp, 5.6 air km E of Four Corners, 1890 m, *Marriott 1584 & Horning* (RM).

Distribution and Ecology:—*Luzula comosa* var. *laxa*, Pacific woodrush, ranges from New Mexico to Saskatchewan, west to California and British Columbia (Fig. 8). It is seldom collected north of 50°N latitude. Localities vary from sea level to 3214 m elevation, in meadows, mesic forests, rocky slopes, and shorelines. Where sympatric with *L. cascadenensis*, *L. comosa* var. *laxa* tends to be on drier soils. Herbarium labels mention many underlying bedrock types including sandstone, argillite, slate, schist, granodiorite, tonalite, basalt, andesite, and ultramafics such as peridotite. Common associates are provided in the appendix.

Typification:—Buchenau (1906) did not list specimens when he described *Luzula comosa* var. *laxa*. However, when previously discussing *L. comosa* (Buchenau 1898), he thanked Frederick Vernon Coville for sending him two specimens of a form with loose spikes and pale flowers. Buchenau (1898: 289) cited the specimens like this: “Unter den Coville’schen Pflanzen befanden sich zwei *Luzula*-Formen mit mässig starker Behaarung, lockeren Aehren und gelb-gefärbten Blüten: Northern Idaho; Coeur d’Atene [Coeur d’Alene] Mountains; along St. Mary’s River; leg. *J. Leiberger*, 27. Juni 1898 (*sineno*). Washington, Hangmann Creek; 460 m; leg. *J. H. Sandberg & J. B. Leiberger*, 16. Mai 1893; Nr. 19.” With the help of the herbarium staff, we made several unsuccessful searches for these specimens at W, where Buchenau’s Juncaceae herbarium resides, diminished somewhat by losses in World War II. Duplicates of this original material were listed in Kirschner *et al.* (2002), and these specimens correspond to the protologue in Buchenau (1906), where he described *L. comosa* var. *laxa* as: “inflorescentia laxa... flores pallide fulvi vel straminei.” It is possible that the original material sent by Coville to Buchenau was a loan, not a gift, and was eventually returned to US. But small differences in the hand-written labels of the various duplicates suggests otherwise. It seems more likely the Buchenau’s original material is not extant, so we have designated a lectotype from the surviving duplicates.

Notes:—The combination of pale tepals, umbellate inflorescence, and bulbous stem base are unique in western North American *Luzula*. Thus *L. comosa* var. *laxa* is usually straightforward to identify. However, on the west slope of the Sierra Nevada, some plants seem to approach *L. macrantha*, with intermediate sized floral parts and darkened tepals. These plants deserve further study. In the vast majority of populations *L. comosa* var. *laxa* and *L. macrantha* are separable by size and color of the tepals (Table 2). In the eastern portion of its range, *L. comosa* var. *laxa* tends to have paler tepals and slightly looser spikes than sympatric *L. multiflora*. Although some shoots, especially young ones, are not obviously bulbous-based, most plants in most populations show the character in the field (Fig. 5), and this helps separate *L. comosa* var. *laxa* from non-bulbous *L. multiflora*.

3. *Luzula macrantha* (Watson 1880: 203) *Zika & B. L. Wilson, comb. et stat. nov.* (Figs. 5C–D, 7B, 9, 11A). *Luzula comosa* Meyer (1823: 21) var. *macrantha* Watson (1880: 203). *Juncooides comosa* (Meyer 1823: 21) Sheldon (1894: 64) var. *macrantha* (Watson 1880: 203) Parish (1895: 59). *Luzula campestris* (Linnaeus 1753: 329) de Candolle (1805: 161) var. *macrantha* (Watson 1880: 203) Fernald & Wiegand (1913: 41).

Type:—UNITED STATES. California: [Contra Costa County], SE of Mt. Diablo, 23 May 1862, *W. H. Brewer 1148* (lectotype, designated by Kirschner *et al.* (2002: 155): GH, isolectotypes K, MO, UC, WS).

Perennial herb, tufted, lacking elongate horizontal rhizomes; stems (7)11–63 cm tall, usually exceeding the leaves, with age usually bulbous-thickened basally; basal sheaths pale brown to red-brown or dull red. Leaves 2–3, distributed

on the proximal 3/4 of the stems; blades herbaceous, 35–150 × 1.5–6 mm, flat, becoming channeled near swollen, blunt, pale or brownish apex, margins spreading-hairy, at least proximally, the margins (at 16×) papillose-serrate; leaf sheaths tight or loose, sparsely to densely long white hairy at V-shaped apex. Vegetative rosettes with blades to 180 × 2–7 mm. **Inflorescences** (1.5)2–11.5 × (0.7)1.5–7 cm, open umbels of (1)2–8(10) spikes (rarely compound). The rays (0.5)1–11 cm, stiffly erect to spreading (slightly arching), spikes 7–20 × 6–11 mm, 4–15 flowered, loose (dense) basally. Proximal inflorescence bract green or reddish, shorter than to longer than the inflorescence, apices swollen, blunt, and discolored, or acute to acuminate. Inflorescence rays subtended by inconspicuous scarious, greenish, or reddish bracts, often fimbriate, shorter than the ray, apices acute to acuminate. Flowers subtended by three scarious acuminate to acute bracteoles, margins erose or hairy, becoming increasingly dissected with age. **Tepals** 6, (3.4)3.6–5.8(6.1) mm, usually dark brown or blackish, stamens 6, filaments (0.2)0.3–0.6 mm, anthers yellow, linear, (1.1)1.2–2.8(3.1) mm, styles straight, persisting, easily broken, (0.7)0.8–2.3 mm. **Capsules** obovate-trigonous, 2–3.2 × 1.4–2.2 mm, apices acute or blunt; with three seeds (1–)1.3–2 mm long (including basal aril) × (0.7)0.8–1.3 mm, fleshy pale aril 0.2–0.4(0.6) mm long, not including the fibrillose base.

Chromosome numbers of *Luzula macrantha* (as *L. comosa* var. *macrantha*) were reported as diploid, $2n = 12$ (Nordenskiöld 1951, 1956).

Additional specimens examined:—CANADA. **British Columbia:** Vancouver Is., Nanaimo, 9 May 2003, *Mann 12* (UBC); Vancouver Is., Parksville, meadow at beach, 3 June 1949, *Nordenskiöld 50-23* (UPS [chromosome voucher $2n = 12$]); Malahat Mountains, 150 m, 22 May 1950, *Krajina & Spilsbury 3994* (UBC); top Mt. Newton, 296 m, 31 May 1966, *Harrison 17.1* (V); near Ruckle Park, E side Salt Spring Is., 15 m, 28 May 2010, *Zika 24879* (WTU); ledges above Eagleridge Drive, near Exit 2 on Route 1, 140 m, 23 June 2008, *Zika 23849* (WTU).

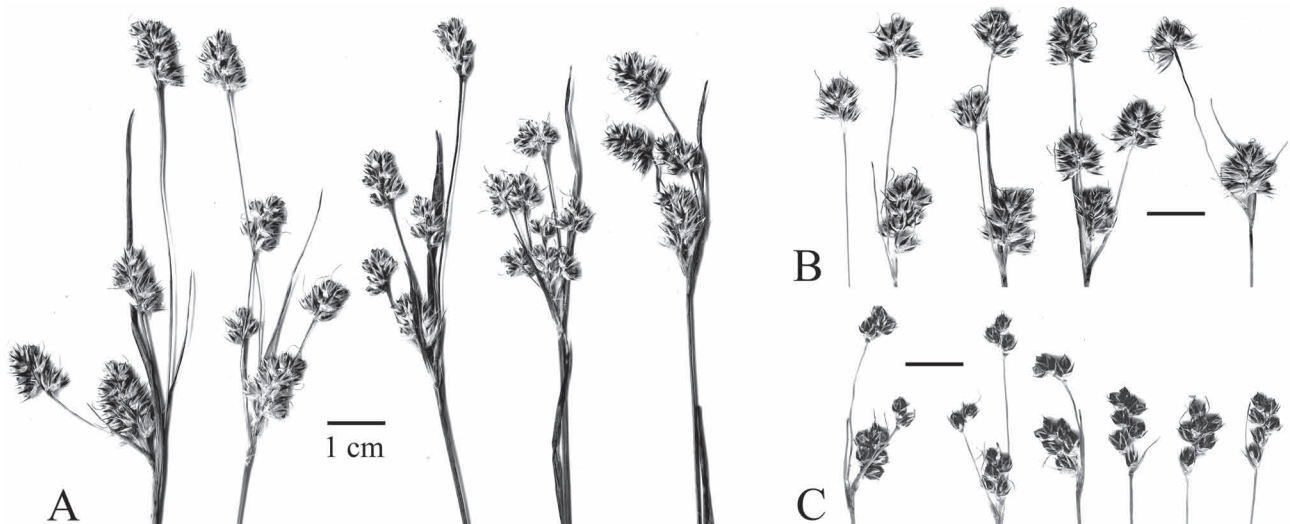


FIGURE 9. Inflorescence variation in *Luzula macrantha*. A. Typical well-developed umbels with elongate rays of unequal lengths (*Zika 25876 & Janeway*). B. Sparse branching in partial shade (*Zika 25533*). C. Depauperate plants with few rays on serpentine soil, spikes loosely-flowered (*Zika 25500*). Scale bars 1 cm.

UNITED STATES. **California:** Butte County, Mosquito Creek between Appleton and Coutelence, 18 May 1919, *Heller s.n.* (MO); N side Dome Trail, c. 3.2 air km NE of Big Bald Rock, 843 m, 29 May 2007, *Ahart 13951* (CHSC); Lake Oroville, McCabe Creek, 265 m, 8 May 2008, *Ahart 14724* (CHSC, NY, OSC, WTU); South Rim Trail, E of Big Chico Creek, Upper Bidwell Park, 329 m, 12 May 2012, *Ahart 18028* (WTU); Concow Road 16 km N of Route 70, 1100 m, 17 June 2009, *Zika 24513* (CHSC, JEPS, OSC, PRA, WTU); 0.8 road km N of dam on Lost Creek Reservoir, 1020 m, 6 July 2011, *Zika 25533* (WTU); E slope Boomer Hill, 701 m, 5 May 2013, *Janeway 11098* (WTU); Calaveras County, Fricot [Ranch] School, 1 May 1962, *Fuller 8310* (CAS); Contra Costa County, Mt. Diablo, Rock City Ridge, 8 May 1933, *Bowerman 2021* (DS, UC); Del Norte County, serpentine slope, French Hill Road near Gasquet, 180 m, 17 May 2010, *Zika 24835* (WTU); 1.6 air km NNW of South Red Mountain, 1210 m, 9 June 2013, *Zika 26196* (WTU); El Dorado County, 4.8 km S of Garden Valley, 17 May 1954, *J. T. Howell 29669* (CAS); N slope Pine Hill, 5.6 km ENE of Rescue, 16 April 1964, *Thorne 33767 & Everett* (RSA); peridotite meadows, chaparral, Traverse Creek confluence with Rock Creek, 686 m, 17 May 2012, *Zika 25876 & Janeway* (WTU); Humboldt County, Titlow Hill Road, 6.8 road km SE of Route 299 at Berry Summit, 1390 m, 3 July 2011, *Zika 25499* (WTU); 1.6 air km S of

Horse Mountain, 1410 m, 3 July 2011, *Zika 25500* (CHSC, GH, V, WTU); Madera County, Bass Lake, Crane Valley Campground, 21 May 1988, *Kelly 213 & Keil* (RSA); Mariposa County, Maxwell Creek, 8 km E of Coulterville on Dogtown Road, 701 m, 12 April 1970, *Breedlove 17399* (CAS); Monterey County, 3.2 km NE of Jamesburg, 9 June 1942, *Durham s.n.* (DS); School Hill, Hastings Reservation, Santa Lucia Mountains, 18 May 1946, *Cook et al. 40* (WS); Napa County, Calistoga, 4 May 1922, *Eastwood 11250* (CAS); Nevada County, 19.3 km S of Grass Valley, 8 May 1937, *Eastwood 4349 & J. T. Howell* (CAS); Bowman Lake Road 1.6 air km N of Highway 20, 1380 m, 23 July 2011, *Ahart 17606* (CHSC); Plumas County, just N of Jansner Park, Quincy, 1036 m, 10 June 1968, *J. T. Howell 44560 & True* (CAS); San Luis Obispo Co., Town Creek near Lime Mountain mine, 26 April 1980, *Walters & Keil 13819* (ASU); San Mateo County, Kings Mountain Road above Woodside, April 1925, *Wiggins 1684* (DS); Santa Barbara County, Camino Cielo near Refugio Pass summit, Santa Ynez Mountains, 686 m, 21 April 1962, *Pollard s.n.* (CAS); Santa Clara County, Stanford, 1 May 1949, *Nordenskiöld 50-22* (UPS [4 chromosome vouchers, all $2n = 12$]); Shasta County, oak woodland, Encanto Way, Redding, 213 m, 15 May 2010, *Zika 24811 & J. K. Nelson* (OSC, WTU); Route 299, 0.2 km E of Stillwater Creek, 191 m, 30 March 2005, *Goldman 3176* (BH); Route 299 just W of Jim Harvey Road, 195 m, 15 May 2010, *Zika 24814 & Nelson* (WTU); Clikapudi Trail, NW of Buck Point, Shasta Lake, 375 m, 16 May 2010, *Zika 24820 & Nelson* (WTU); Siskiyou Co., 3 air km SSE of Castle Dome, 640 m, 18 May 2012, *Zika 25885* (WTU); S end of Dunsmuir, 730 m, 18 May 2012, *Zika 25887* (WTU); Trinity County, Mad River, 17.7 km SE of Ruth, 5 June 1939, *Cantelow 2617* (CAS); Tuolumne County, Phoenix Lake Road, 4.5 km NE of Highway 108, between Sonora and Twain Harte, 771 m, 29 May 1971, *Wiggins 21358* (DS); Yuba County, Challenge Cut-off, 2.5 air km NE of Brownsville, 755 m, 22 June 2010, *Zika 24980* (WTU); 2.7 air km WSW of Ruff Hill, Brownsville, 665 m, 16 May 2012, *Zika 25869 & Janeway* (WTU). **Oregon:** Douglas County, ridge by Bushnell Rocks, 596 m, 7 June 2008, *Wilson 14622* (WTU); Gallagher Ridge, Gallagher Canyon Road, 324 m, 21 June 2008, *Wilson 14655* (OSC); Jackson County, between Logan Drive and Ditch Road, Ashland, 625 m, 15 May 2010, *Zika 24810 & Lang* (MO, MONTU, NY, OSC, WS, WTU); Josephine County, Grants Pass, 24 April 1887, *T. Howell s.n.* (ORE); Route 199 just S of Cave Junction, 24 April 1987, *Straley 4119* (UBC); Forest Road 2512 near Chrome Ridge, 1341 m, 27 June 1998, *Gage 4730* (WTU); Marion County, damp oak savanna, S of Mission Street near Pringle Creek, Salem, 55 m, 14 May 2012, *Zika 25841* (WTU). **Washington:** Jefferson County, NW side Toandos Peninsula, Camp Discovery Road, Dabob Bay, 10 m, 3 May 1986, *Zika 9553* (OSC); Klickitat County, oak savannah near Lyle Balch Cemetery above Catherine Creek Road, 190 m, 24 May 2009, *Zika 24445* (WTU); Canyon Road near Johnson Road, 630 m, 24 May 2009, *Zika 24447* (WTU); Mason County, prairie 3 mi N of Shelton, 9 May 1940, *Gould 1137* (DS, GH, MO, PH); Pierce County, dry prairie N side of Muck Creek, Fort Lewis, 120 m, 4 June 2001, *Zika 16162A & Weinmann* (WTU); Skamania; Pierce County, oak woodland near start of Augspurger Trail, Columbia River Gorge, 60 m, 24 May 2009, *Zika 24443* (OSC, WTU); Thurston County, dry prairie remnant, E side Interstate 5 at Scatter Creek Rest Area, 60 m, 20 May 2009, *Zika 24402* (OSC, WS, WTU); near Mima Mounds Natural Area, 60 m, 3 June 2009, *Zika 24458* (OSC, RSA, UC, WS, WTU); Whatcom County, hill NW of Newhalem, Ross Lake National Recreation Area, 188 m, 4 June 2011, *Legler 11917* (WTU).

Phenology:—The capsules ripen from April to July.

Distribution and Ecology:—*Luzula macrantha*, large-anthered or large-flowered woodrush, is found from Vancouver Island south to southern California (Fig. 10), mainly west of the crest of the Cascade Range and Sierra Nevada. Inland populations are found on low elevation grassy balds around Ross Lake in the interior of Whatcom County, Washington. In the Columbia River Gorge *L. macrantha* is a frequent member of the understory of oak woods, well to the east of the range of *L. subsessilis* (Fig. 4). *Luzula macrantha* is widespread in open oak or pine forest, chaparral, bluffs, and openings in the Klamath Mountains of Oregon and California, and common at lower elevations on the western slope of the Sierra Nevada. In California *Luzula macrantha* ranges far to the east of the coast and coastal mountain populations of *L. subsessilis* (Fig. 4), but does not cross the Sierra crest and has not been collected in Nevada. Recorded elevations span sea level to 1341 m. Herbarium labels mention the underlying bedrock is mudstone, sandstone, meta-sedimentary, gabbro, diorite, granodiorite, or peridotite. Common associates are provided in the appendix.

Notes:—Recent western North American floras combined the concepts of *Luzula macrantha* and *L. subsessilis* under the latter name or under *L. comosa* (Table 1). *Luzula macrantha* is distinguished from *L. comosa* by its longer, darker tepals, as well as its longer styles and anthers (Table 2). Where *L. subsessilis* is sympatric with the more western populations of *L. macrantha*, the two can be readily separated by the shape of the inflorescence, as well as measurements of the tepals, anthers, and styles (Table 2). Depauperate individuals of *L. macrantha*, in deep shade or on harsh serpentine sites, can have smaller flower parts than typical, or an inflorescence reduced to a single spike (Fig. 9B on left, Fig. 9C on right). Such plants still show darker tepals than *L. comosa* var. *laxa*, and some plants in the

population develop more inflorescence branching than *L. subsessilis*. In the north, poorly developed individuals of *L. macrantha*, if sampled adequately, show a more bulbous base than sympatric *L. multiflora*.

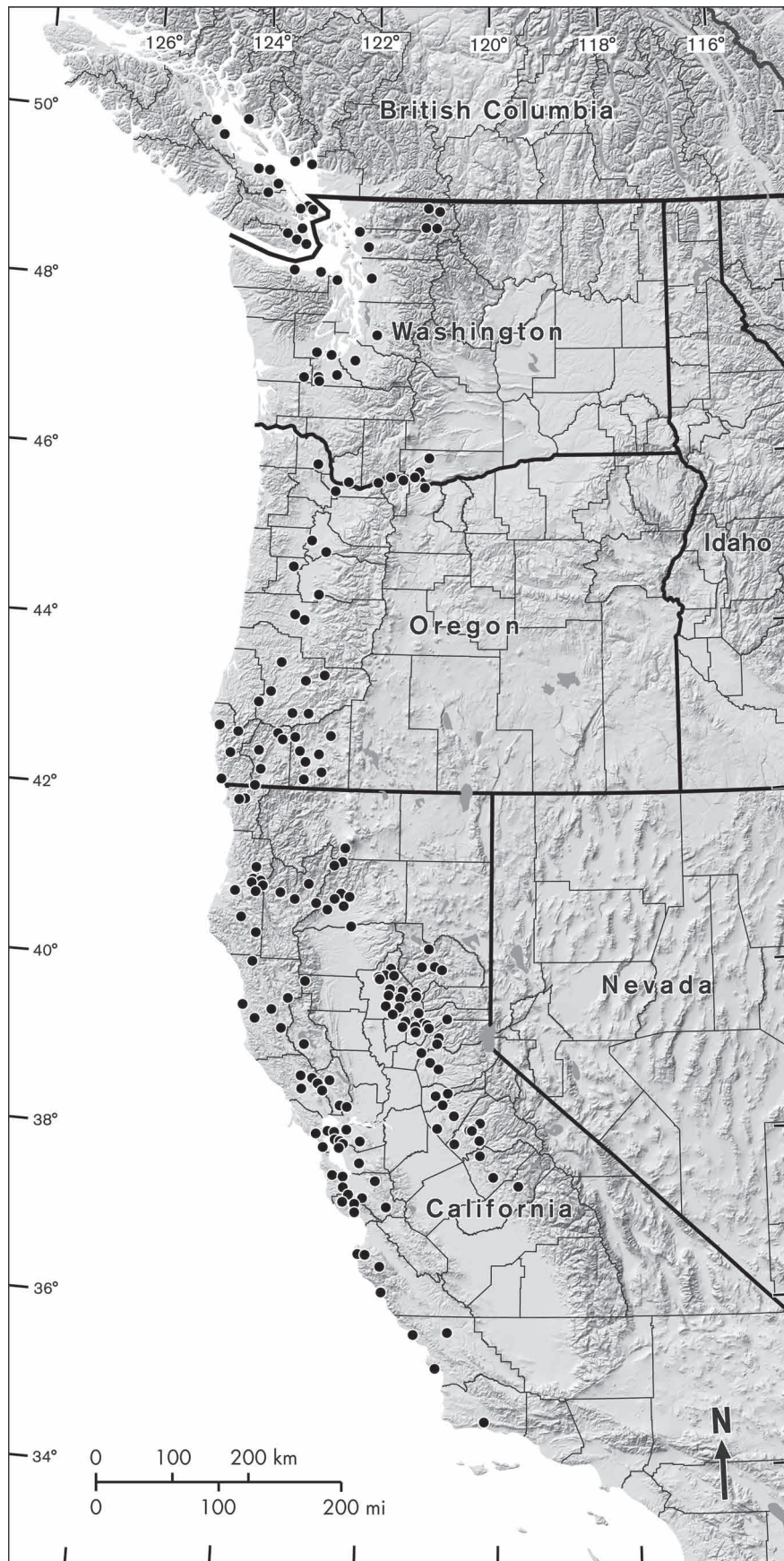


FIGURE 10. Distribution of *Luzula macrantha*, plotted from herbarium specimens seen in this study.

In mixed populations of *Luzula macrantha* and *L. subsessilis* we observed a few morphological intermediates (Fig. 11), which we presume to be hybrids (e.g., *Zika* 24862 [WTU] from Grays Harbor County, Washington). Our suggestion that these are hybrids is based on morphological and ecological data; we have no results from genetic or molecular investigations to report. Morphological intermediacy was observed in artificial hybrids in European members of the group that had the same ploidy levels (Nordenskiöld 1956, 1971); the putative hybrid plants are intermediate and the putative parents have the same ploidy levels. The presumed hybrids show the umbellate inflorescence of *L. macrantha*, and the peduncled spike from the distal leaf axil characteristic of *L. subsessilis* (Table 2). In addition, the putative hybrids show a terminal inflorescence more congested than in *L. macrantha*, but more open than in *L. subsessilis*. Neither of the putative parents shows this range of morphological variation when in isolation. We note there were no other closely related species in the area that might have been involved in hybridization. And the parents and putative hybrids were maturing more or less simultaneously, so there was no apparent phenological barrier to crossing. A more detailed study of potential hybrids like these would be useful, to see if there was reduced fertility and if there was backcrossing. There is also the intriguing question of how these two species might have evolved with partial sympatry if there is little barrier to gene flow.

4. *Luzula subsessilis* (Watson 1880: 203) Buchenau (1898: 290). (Figs. 5E, 7C, 11B, 12). *Luzula comosa* Meyer (1823: 21) var. *subsessilis* Watson (1880: 203). *Juncoides comosa* (Meyer 1823: 21) Sheldon (1894: 64) var. *subsessilis* (Watson 1880: 203) Sheldon (1894: 64). *Juncoides subsessilis* (Watson 1880: 203) Piper (1915: 91).

Type:—[UNITED STATES]. California: Geological Survey of California, [San Francisco Co., San Francisco], Fort Point, June 1862, *H. N. Bolander 1578* (lectotype, designated by Kirschner *et al.* (2002: 155): GH, isotypes GH, UC).

Luzula comosa Meyer (1823: 21) var. *congesta* Watson (1880: 203). Not *L. congesta* (Thuillier 1799: 178) Lejeune (1811: 169). Not *Juncoides campestris* (Linnaeus 1753: 329) Kuntze (1891: 724) var. *congesta* (Thuillier 1799: 178) Sheldon (1894: 64). Not *J. campestris* (Linnaeus 1753: 329) Kuntze (1891: 724) subsp. *congesta* (Thuillier 1799: 178) Piper (1915: 92).

Type:—UNITED STATES. California: near San Francisco, collected by Dr. J. M. Bigelow, surgeon and botanist to the expedition, Lieut. A. W. Whipple's Exploration for a Railway Route, from the Mississippi River to the Pacific Ocean, near the 35th parallel of latitude, in 1853–54 [April 1854], *J. M. Bigelow s.n.* (lectotype, here designated: GH, isolectotype PH).

Perennial herb, tufted, lacking elongate horizontal rhizomes; stems (4.5)7–61.5 cm, usually exceeding the leaves, with age usually bulbous-thickened basally; basal sheaths pale brown, rarely dull red or red-brown. Leaves 2–5, distributed on the proximal 3/4 of the stems; blades herbaceous, 10–170 × 1.5–8 mm, flat, becoming channeled near swollen, blunt, pale or brownish apex, margins spreading-hairy, at least proximally, the margins (at 16×) papillose-serrate; leaf sheaths tight or loose, densely long white hairy at V-shaped apex. Vegetative rosettes with blades 30–180 × 1–6 mm. **Inflorescences** terminal, 1–4 × 0.5–2.5 cm, dense or congested heads of 1–9 sessile or subsessile spikes. Occasionally with a peduncled spike from the distal leaf axil, on peduncles (0.5)1–11 cm, stiffly erect to slightly arching. Spikes 5–18 × 5–8 mm, 4–18 flowered, loose to dense basally. Proximal inflorescence bract green or reddish, shorter than to longer than the inflorescence, apices swollen, blunt, and discolored, or acute to acuminate. Secondary inflorescence bracts inconspicuous to prominent, scarious, greenish, or reddish, often fimbriate, often shorter than the inflorescence, apices swollen, blunt, and discolored, or acute to acuminate. Flowers subtended by three scarious acuminate to acute bracteoles, margins erose or hairy, becoming increasingly dissected with age. **Tepals** 6, 2.1–3.7(4) mm, dark brown or blackish, stamens 6, filaments 0.3–0.7 mm, anthers yellow, linear, 0.4–1.1(1.3) mm, styles straight, persisting, easily broken, 0.1–0.7 mm. **Capsules** trigonous, obovate to elliptic or broadly elliptic, 1.8–2.6 × 1.2–2.4 mm, apices acute or blunt; with three seeds (0.9)1.2–1.85 mm long (including basal aril) × 0.7–1.1 mm, fleshy pale aril 0.2–0.6 mm long, not including the fibrillose base.

Chromosome counts for *L. subsessilis* were all diploid, $2n = 12$ (Nordenskiöld 1951).

Additional specimens examined:—CANADA. **British Columbia:** Vancouver Is., Uplands Park near Cattle Point, Oak Bay, 15 m, 19 May 1967, *Harrison 90.2* (V); Victoria, 24 May 1887, *Macoun 62456* (BH, CU); Victoria, above McNeil Bay, 60 m, 21 May 1950, *Krajina 3948 & Spilsbury* (UBC); Victoria, Beacon Hill, 15 m, 29 May 2010, *Zika 24885* (CHSC, PRA, WTU); Mill Hill, Langford, 1 June 1967, *Harrison 73.1* (UBC); Whiffin Spit, near Sooke, 9 May 1966, *Beamish s.n.* (UBC); Renfrew District, June–July 1901, *Rosendahl & Brand 33* (DS, MO, PH, RM); dunes near Cordova Spit, Saanich Peninsula, 5 m, 30 May 2010, *Zika 24886* (OSC, V, WTU); Mitlenatch Is., rock bluffs, 19 May 1963, *Haddow 47* (V); between Beaver Point and Eleanor Point, Salt Spring Is., Gulf Is., 15 m, 28 May 2010, *Zika 24880* (DAO, NY, UPS, WTU); Halibut Is., 11 May 1963, *Tompka s.n.* (UBC).



FIGURE 11. Inflorescence variation in a putative hybrid *Luzula*. A. *Luzula macrantha*, showing umbellate inflorescences with rays of unequal lengths (Zika 25533). A × B. *Luzula macrantha* × *subsessilis*, showing congested umbels and some elongate peduncles from lower nodes (Zika 24862). B. *Luzula subsessilis*, showing condensed terminal inflorescence and elongate peduncles from lower nodes, although these are not present on all individuals (Zika 18435).

UNITED STATES. **California:** Del Norte County, Crescent City, 20 April 1892, *T. Howell* 1478 (MO, UC); near Phillipsville, 15 m, 2 April 1927, *Tracy* 7878 (UC); bluffs S of Crescent City, 22 April 1933, *Tracy* 12030 (UC); Humboldt County, Ocean Beach, Humboldt Bay, sand dunes, 24 April 1904, *Tracy* 2032 (UC); 1 air km SSW of Horse Mountain, 1310 m, 3 July 2011, *Zika* 25494A (WTU); Marin County, Sausalito, 1881, *Greene s.n.* (CAS); Olema, 31 March 1894, *Davy* 687 (PH); Mt. Tamalpais, 31 March 1917, *Jepson* 6857 (JEPS); Angel Is., S ridge of Mt. Ida, 183–238 m, 1 May 1967, *Raven & Johnson* 21165 (DS); Inverness Ridge, W of Inverness, 15 May 1949, *J. T. Howell* 25317 (GH, RSA, UC [chromosome voucher $2n = 12$]); W end Lucas Valley, 27 April 1969, *J. T. Howell* 45557 (CAS); hill above Tiburon, 137 m, 25 March 1961, *Peñalosa* 1196 (CAS); Road A104 just W of Jewell, 17 April 1982, *Boze* 418 (CAS); Mendocino County, Redwood Valley N of Calpella, 213 m, 16 April 1938, *Tracy* 15710 (RM, UBC, UC); N of Fort Bragg, Cleone Lake, 19 May 1946, *Mason* 12781 (DS, UC); near Howard Lake, 10 May 1980, *Jokerst* 681 (CHSC); Caspar Little Lake Road, 0.5 km E of Route 1, 90 m, 21 June 2010, *Zika* 24961 (WTU); Monterey County, Pacific Grove in pine woods, 26 March 1903, *Heller* 6467 (BKL, DS, POM); San Francisco County, San Francisco, 1892, *Bioletti s.n.* (PH); windswept slopes above Baker's Beach, 91 m, 28 March 1954, *Raven* 6499 (CAS); grassy hill between Lands End and Golden Gate Bridge, 18 March 1956, *Raven* 8869 (CAS); Presidio golf links, 7 April 1956, *Rubtzoff* 2174 (CAS); gully S of Stanley Drive, E of Lake Merced, 20 April 1956, *Rubtzoff* 2271 (CAS); N slope Bay View Hills, 10 June 1956, *J. T. Howell* 31552 (CAS); San Luis Obispo County, Cambria, 30 June 1964, *J. T. Howell* 40859 (CAS); Arroyo de la Cruz, windswept coastal hills, 18 May 1980, *Keil* 14026 *et al.* (ASU); Hearst Ranch, 11.3 air km N of San Simeon, 61 m, 11 April 1987, *Ertter* 6847 *et al.* (NY, RSA, UC); San Mateo County, Guadalupe Canyon Parkway W of Radio Road junction, 28 March 1976, *Rubtzoff* 8450 (WTU); Colma Canyon, 18 April 1931, *Jussel s.n.* (CAS); E slope San Bruno Mountain, 60 m, 19 March 1958, *Thomas* 7060 (DS); SE shore Alpine Pond, Santa Cruz Mountains, 660 m, 1 May 2010, *Zika* 24790 (CHSC, DAV, MO, UCR, V, WS, WTU); Santa Barbara County, Santa Barbara, April 1924, *Hoffmann s.n.* (CAS); Camino Cielo, about 3.2 km W of San Marcos Pass, Santa Ynez Mountains, 762 m, 25 April 1955, *Pollard s.n.* (CAS, RSA); hillside near Torrey pine grove, Santa Rosa Is., 6 April 1941, *Moran* 806 (DS, NY, RSA); Cherry Canyon, Santa Rosa Is., 61 m, 5–10 April 1960, *Blakely* 3146 (CAS, RSA); lower Canada Christy drainage, Santa Cruz Is., 107 m, 21 May 1994, *Junak* SC-3988 (RSA); Santa Clara County, Stanford, 26 April 1949, *Nordenskiöld* B25 (UPS [chromosome voucher $2n = 12$]); Santa Cruz County, Swanton Road, NE of Greyhound Rock, 100 m, 3 May 2010, *Zika* 24801 (CAS, PRA, RSA, UTEP, WTU); Sonoma County, 6.4 km W of Two Rocks, 30 April 1934, *Lee et al.* 764 (JEPS); Laguna de Santa Rosa, E of Cunningham, near Llano Road, 11 April 1962, *Rubtzoff* 4793 (NY, WTU); Bennett Mountain Lake, 26 May 1963, *Rubtzoff* 5135 (WTU); Upper Green Valley Marsh, 17 April 1974, *Rubtzoff* 7369 (WTU); Trinity County, junction Mad River Rock Lookout Station Road and Highway 36, 11 June 1948, *Ferris & Lorraine* 11679 (DS, ORE, RSA, UC, WTU). **Oregon:** Benton

County, unplowed lowland floodplain prairie 0.8 km E of Muddy Creek, Finley National Wildlife Refuge, 21 June 1972, *Mika 157* (OSC); Cherry Creek Road W of Monroe, 29 April 1983, *Scofield s.n.* (ORE); Jackson-Frazier Wetland, 69 m, 28 May 1995, *Halse 4892* (OSC); meadow, Circle Boulevard, Corvallis, 110 m, 14 May 2010, *Zika 24804* (CAS, CHSC, PH, PRA, WS, WTU); SE slope Bald Hill, Corvallis, 130 m, 19 May 2012, *Zika 25892 & Brainerd* (DAO, US, W, WTU); Clatsop County, Seaside, 28 June 2008, *Sheldon 12259* (ORE); Camp Rilea stabilized dunes, 3 m, 23 June 2009, *Wilson 15606 et al.* (OSC); Columbia County, St. Helens, 50 m, 1 June 2010, *Zika 24894* (OSC, RSA, WTU); Coos County, bench near coast, 9.7 km S of Bandon, 1 June 1952, *Stewart 6155 et al.* (OSC); W end Croft Lake Road, 15 m, 17 May 2010, *Zika 24842* (CHSC, RSA, WTU); Curry County, Rogue River Canyon, overlooking the mouth, Two Mile Creek, 1 May 1948, *Baker 5256* (ID); Douglas County, near N shore North Umpqua River, above North Bank Road, 180 m, 14 May 2010, *Zika 24807* (CHSC, NY, OSC, UC, WS, WTU); Jackson County, 14.5 km SE of Grants Pass, 16 May 1924, *Sherwood 252* (WILLU); Josephine County, 1.5 air km ESE of Lone Mountain, 21 June 2010, *Zika 24935* (WTU); meadow near corner Monument Drive and Camp Jay Road, 360 m, 14 May 2011, *Zika 25850* (ASC, CHSC, TAES, UCR, UTEP, WTU); Lane County, Spencer Butte, 5 May 1935, *Brown 368* (ORE); Heceta Beach, dune, 3 m, 21 April 1938, *Detling 2498* (ORE); dunes, mouth of Sutton Creek, 22 April 1938, *Detling 2511* (ORE); grassy bluff just N of Rock Creek, 26 km N of Florence, 21 May 1977, *Crosby 1204* (OSC); NW slope Mt. Pisgah, 275 m, 14 May 2010, *Zika 24805* (GH, MO, OSC, PRA, RSA, WTU); Lincoln County, D Lake, 23 May 1931, *Peck 16336* (WILLU); dunes between Hidden Lake and the ocean, 3.2 km N of Waldport, 21 April 1956, *Barkley s.n.* (OSC, WS); Otter Crest, rocky headland, 61 m, 1 May 1938, *Detling 2585* (ORE); sand dune 3 km S of mouth of Yaquina River, 5 m, 18 May 2010, *Zika 24845* (BRIT, NY, RSA, UBC, V, WTU); Marion County, oak savanna, S of Mission Street near Pringle Creek, Salem, 55 m, 14 May 2012, *Zika 25843* (TAES, UTEP, WTU); Yamhill County, Coast Range at Walker Flat, 552 m, 13 June 1985, *Halse 3061* (OSC, RSA). **Washington:** Clark County, Green Mountain Resort Conservation Easement, 1 May 1998, *Habegger 345* (WTU); Grays Harbor County, 1.6 air km SE of Oakville, 30 m, 21 May 2010, *Zika 24855* (MICH, UBC, WTU); 6 air km WNW Oakville, 25 m, 21 May 2010, *Zika 24861* (DAO, DAV, NEB, PRA, TEX, WTU); Island County, near W shore Cranberry Lake, Whidbey Is., 3 m, 20 May 2000, *Zika 14999* (WTU); forested dunes 1.6 km S of Cranberry Lake, 5 m, 26 May 2010, *Zika 24876* (K, KSC, MONTU, RSA, V, WS, WTU); Ebey's Landing, 4 m, 30 April 2004, *Legler 1522* (WTU); Jefferson County, Protection Is., 54 m, 3 May 2006, *Weinmann 1008* (WTU); Lewis County, Drews Prairie, 1.6 km S of Winlock-Toledo Road, 90 m, 1 June 2010, *Zika 24892* (GH, KANU, MONT, UPS, USCH, W); Pacific County, Willapa Bay National Wildlife Refuge, dunes, 2 m, 17 May 2007, *Giblin 851 et al.* (WTU); San Juan County, Aleck Rock, S of Lopez Is., 26 April 2005, *Arnett 05–26* (WTU); Battleship Is., 28 May 2009, *Giblin 2846* (WTU); Boulder Is., 26 April 2005, *Dunwiddie 05–41* (WTU); Castle Is., 28 April 2005, *Legler 2538* (WTU); Coon Is., 12 m, 28 April 2006, *Dunwiddie 06–72* (WTU); Fawn Is., 15 m, 31 May 2006, *Dunwiddie 06–274* (WTU); Little McConnell Is., 28 April 2006, *Legler 3280B* (WTU); Weed Point, Flattop Is., 2 m, 31 May 2006, *Marschner 06–73* (WTU); Flint Beach Is., 27 April 2005, *Zika 20503* (WTU); Gossip Is., 28 May 2009, *Legler 11289* (WTU); Henry Is., salt meadows near Henry Bay, 1 m, 9 June 2001, *Zika 16233* (WTU); Iceberg Point, Lopez Is., 17 May 1995, *Naas 5728* (WTU); McConnell Is., 1 m, 30 May 2006, *Wyllie-Echeverria 06–19* (WTU); Ripple Is., 27 April 2006, *Gilbert 06–89* (WTU); Rum Is., 29 May 2005, *Johanson & Johanson 05–56* (WTU); Friday Harbor Marine Laboratory, mossy bald, San Juan Is., 7 May 1997, *Gage SG–2784* (WTU); Skull Is., 12 m, 30 May 2006, *Camp 06–55* (WTU); Victim Is., 15 m, 1 June 2006, *Camp 06–106A* (WTU); Yellow Is., E and S shores, 7 m, 5 May 2002, *Zika 16844* (WTU); Skagit County, rocky knoll 8 km S of Anacortes, 15 May 1938, *Hitchcock 3437* (DS, RSA); near Canoe Pass, Fidalgo Is., 122 m, 13 May 1939, *Hitchcock 4664 & Martin* (BH, DS, GH, WS); Rosario Beach, Deception Pass, 259 m, 13 May 1965, *Dietel 583* (WS); Dot Is., 21 m, 1 May 2007, *Legler 3771* (WTU); Saddlebag Is., 5 m, 23 May 2006, *Dunwiddie 06–143* (WTU); Vendovi Is., 1 June 2011, *Dunwiddie 2011–55* (WTU); Thurston County, Mound Prairie, 55 m, 18 May 2010, *Zika 24847* (DAO, K, PRA, WTU); Scatter Creek Rest Area, Interstate 5, 60 m, 1 June 2003, *Zika 18435* (ASC, BM, PH, S, UPS); near Mima Mounds Natural Area, disturbed dry prairie remnant, 60 m, 3 June 2009, *Zika 24459* (KSC, WTU); Rock Prairie, 4 air km NNW of Bucoda, 75 m, 21 May 2010, *Zika 24852* (WTU); 2 air km E of Offutt Lake, 85 m, 21 May 2010, *Zika 24848* (CHSC, MO, RSA, WTU); Whatcom County, Lummi Is., 28 April 1939, *Muenschner 9713* (BH, GH, WS).

Phenology:—The capsules usually mature from April to June.

Distribution and Ecology:—*Luzula subsessilis*, prairie woodrush, ranges from Vancouver Island south to the Channel Islands of southern California (Fig. 4), and is restricted to the coast, Puget Trough, and coast mountains. It favors lightly vegetated marine sand dunes, open oak or pine forest, edges, ledges, coastal sage scrub, chaparral after fires, and native grassland remnants. Populations were recorded from sea level to 1310 m elevation. Herbarium labels noting the underlying bedrock types mentioned sandstone, argillite, slate, greenstone, schist, basalt, granodiorite, and serpentinite. Common associates are provided in the appendix.

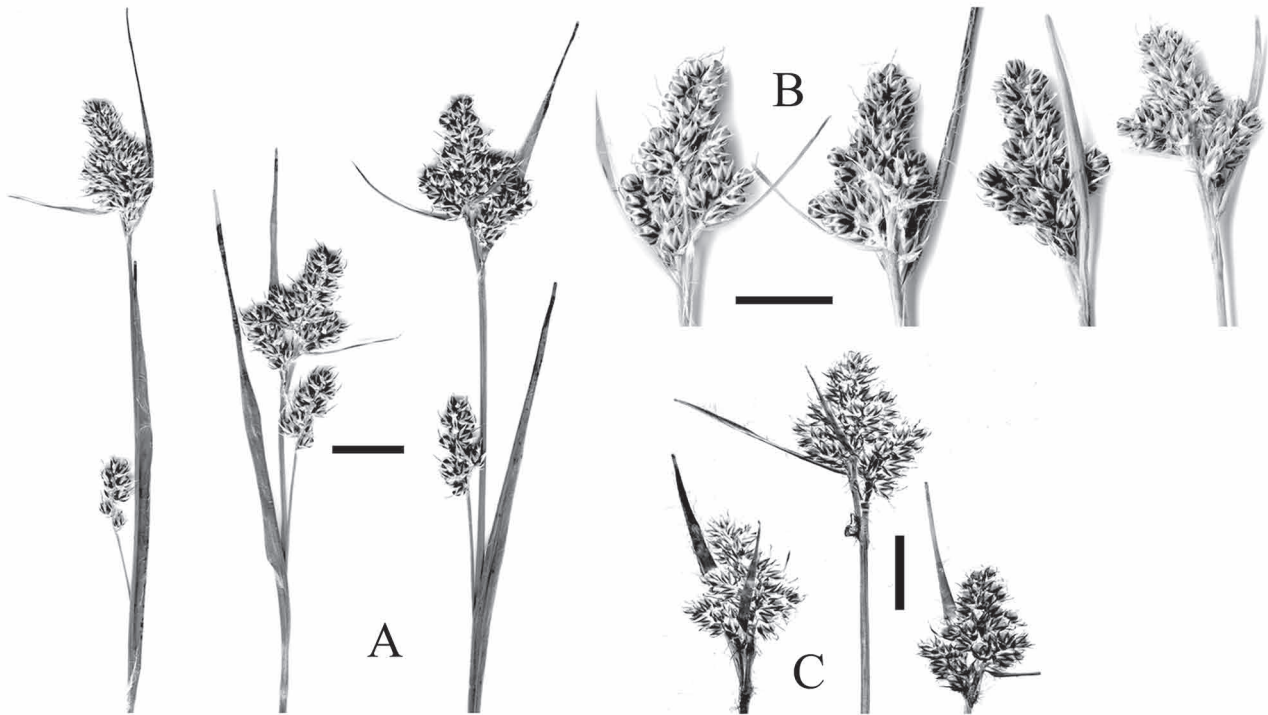


FIGURE 12. Inflorescence variation in *Luzula subsessilis*, with condensed terminal inflorescences, and occasional elongate peduncles from lower nodes. A. *Zika* 18435. B. *Zika* 25892 & *Brainerd*. C. *Zika* 24847. Scale bars 1 cm.

Typification:—Typification of *Luzula subsessilis* presented problems. Kirschner *et al.* (2002: 155) chose a *Bolander* gathering at GH as a lectotype for *L. subsessilis*, using the date 1866. A duplicate at GH, hand labeled by Watson as “1578” and “*L. comosa* var. *congesta* Watson,” has a pre-printed label that states: “Geological Survey of California, 1860–62, Coll. *W. H. Brewer*.” We believe the collector on the pre-printed label was an error, and the specimen was gathered by H. N. Bolander, not W. H. Brewer. A check of collections databased by the Consortium of California Herbaria (2014) shows no Brewer collections numbered 1578, and shows Bolander gatherings from the shores of Fort Point and San Francisco numbered 1568, 1572, 1576, and 1578. The dates on the labels are given variously as 1860–1862, 1860–1867, 1866, or more precisely as June 1862 for gatherings from Fort Point in San Francisco (e.g., *Bolander* 1568 [UC, 2 sheets]).

A second point is that our study of Watson’s annotations on his original material at Harvard shows that our concept of *Luzula subsessilis* includes Watson’s *L. comosa* var. *subsessilis* as well as his *L. comosa* var. *congesta*. The relevant collections came to light recently at GH, and supersede the interpretation of Kirschner *et al.* (2002), which placed var. *congesta* Watson (1880: 203) in synonymy under *L. comosa* var. *comosa*, another coastal taxon with a congested inflorescence. Our choice of a lectotype for var. *congesta*, a Bigelow specimen at GH, was annotated by Watson, first to “var. *congesta* Meyer,” then to “var. *congesta* Watson,” mirroring his nomenclature in 1880. It also matches the protologue: “spikes several, sessile, and close, forming a somewhat pyramidal head, perianth brown.” Specimens at GH that Watson annotated to var. *congesta* have the characteristic dark brown to black tepals found in *L. subsessilis*, and they do not have the usually scarious or stramineous to very pale brown tepals found on *L. comosa* var. *comosa*. Kirschner *et al.* (2002) mentioned only one gathering as original material for var. *congesta*, “California, *D. Douglas* s.n. K,” with a duplicate at W. We could not find the specimens at Kew or Vienna to re-examine them, but a duplicate at GH is labeled “California, Douglas,” in Asa Gray’s handwriting. This would be among the original materials Watson had at hand when describing var. *congesta*, and Watson’s hand-written annotation of “var. *congesta*” appears on two other specimens on the sheet, which has a total of four gatherings of *L. subsessilis* from California, mounted together.

Habit:—*Luzula subsessilis*, like the other bulb-based members of sect. *Luzula* in western North America, can rarely produce a vertical rhizome. Fernald and Wiegand (1913) mentioned this, and we illustrate it (Fig. 5E). Field investigation reveals that most plants in a population do not produce such a rhizome, so its production is facultative, and perhaps a response to soil movement and burial. The rhizomes are essentially vertical, unlike those of *L. cascadenis* or *L. campestris*. Whether or not the rhizomes are present, the shoots bases become swollen.

Key to the species of *Luzula* sect. *Luzula* in western North America

The measurements for *Luzula multiflora* differ in separate leads in the key, because by necessity we are including what we believe are different subspecies or species under the name *L. multiflora*. The *L. multiflora* complex in North America requires further research before a stable and accurate classification of its members is established.

1. Plants with horizontal rhizomes, lacking bulbous bases2
- 1- Plants caespitose, bases often bulbous, rarely with short vertical rhizomes5
2. Seeds 0.95–1.6 mm long, including aril 0.15–0.45 mm3
- 2- Seeds usually 1.6–2.1 mm long, including aril 0.4–0.8 mm4
3. Stem leaves usually < 5 mm wide; seeds (0.95)1.1–1.6 mm long including aril; tepals pale to dark brown; montane wet meadows and peatlands; southern Washington south to California, east to western Montana *L. cascadenensis*
- 3- Stem leaves > 5 mm wide; seeds 1.2–1.3 mm long including aril; tepals dark brown to blackish; maritime habitats in coastal Alaska and northeastern Asia *L. kobayasii*
4. Anthers 0.6–0.9 mm; tepals 2.5–3.1 mm; styles 0.3–0.6 mm; low elevation coastal wet meadows and peatlands; northern Vancouver Island north to Alaska *L. multiflora*
- 4- Anthers (1)1.5–2 mm; tepals 2.8–4.2 mm; styles 0.5–1.5 mm; low elevation uplands and disturbed soils
..... *L. campestris* subsp. *campestris*
5. Tepals pale, whitish to pale brown or medium brown *L. comosa* (with 2 varieties) 6
- 5- Tepals dark brown to blackish7
6. Inflorescences dense, unbranched; range coastal *L. comosa* var. *comosa*
- 6- Inflorescences usually umbellate, branched; range coastal and inland *L. comosa* var. *laxa*
7. Inflorescences dense, unbranched8
- 7- Inflorescences branched, umbellate13
8. Habitat low to moderate elevation, non-arctic sites, including coastal southern Alaska 9
- 8- Habitat alpine and arctic sites11
9. Stem base not bulbous; stem leaves usually 5–8 mm wide; seeds up to 1.4 mm long, including aril often 0.2–0.3 mm long; coastal Alaska and northeastern Asia *L. kobayasii*
- 9- Stem base bulbous; stem leaves usually < 6 mm wide; seeds up to 1.85 mm long, including aril 0.15–0.6 mm long; southwestern British Columbia south to California10
10. Fertile culms usually lacking a long-peduncled axillary spike from a lower node; tepals medium brown; seeds 0.6–0.9 mm wide
..... unusually dark *L. comosa* var. *comosa*
- 10- Fertile culms often with a long-peduncled axillary spike from a lower node; tepals dark brown to blackish; seeds 0.7–1.1 mm wide *L. subsessilis*
11. Anthers 0.6–1.3 mm; seeds 0.8–1 mm wide, 1.5–1.8 mm long, including aril 0.3–0.5 mm; base bulbous *L. multiflora*
- 11- Anthers 0.3–0.6 mm; seeds 0.5–0.7 mm wide, 0.9–1.2 mm long, including aril 0.1–0.25 mm; base not bulbous 12
12. Leaves 3–4 mm wide; tepals 2.3–2.9 mm; seed arils 0.1–0.25 mm; Sierra Nevada Range of California and Wallowa Mountains of Oregon *L. orestera* Sharsmith (1958: 125)
- 12- Leaves 1.4–3 mm wide; tepals 1.9–2.5 mm; seed arils 0.1–0.15 mm; northern British Columbia, Alaska, and east across northern Canada *L. groenlandica* Böcher (1950: 18, pl. 1)
13. Plant base not bulbous; flowers and fruits dense, compact, and contiguous at spike bases 14
- 13- Plant base bulbous; flowers and fruits at base of spikes dense or somewhat scattered or loosely arranged at spike bases15
14. Stem leaves 4.5–8 mm wide, usually broader than basal leaves; basal leaves 5–6 mm wide; inflorescence bracts often prominent; rays of umbel often with secondary terminal branching; pedunculate clusters often with 2–4 subclusters; coastal southern Alaska, the Aleutian Is., Kamchatka, and the northern Kurile Is *L. kobayasii*
- 14- Stem leaves usually 1–5 mm wide, usually narrower than basal leaves; basal leaves 1.8–6 mm wide; inflorescence bracts not prominent; rays of umbel rarely with secondary branching; pedunculate clusters usually simple; widespread, coastal Alaska south to Oregon and east across North America, Eurasia *L. multiflora*
15. Anthers (1.1)1.2–2.8(3.1) mm; longer tepals usually 3.6–5.8(6.1) mm; styles (0.7)0.8–2.3 mm; coastal, foothills and lower mountain slopes, southwestern British Columbia south to California *L. macrantha*
- 15- Anthers 0.5–0.9(1.1) mm; longer tepals 2.2–4.2 mm; styles 0.2–0.9(1.1) mm; coastal lowlands and montane to subalpine meadows, inland to Alberta, South Dakota, and New Mexico16
16. Some spikes with slightly loose or scattered distal flowers/fruits; coastal, foothills, and montane
..... unusually dark forms of *L. comosa* var. *laxa*
- 16- Spikes dense distally; subalpine meadows *L. multiflora*

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Appendix 1:—Common associates for members of the *Luzula comosa* complex, based on herbarium labels and field notes.

1. ***Luzula cascadiensis***: *Abies magnifica* A. Murray bis, *Agrostis scabra* Willd., *Allium validum* S. Watson, *Calamagrostis canadensis* (Michx.) P. Beauv., *Carex aurea* Nutt., *C. bolanderi* Olney, *C. echinata* Murray, *C. feta* L. H. Bailey, *C. fissuricola* Mack., *C. laeviculmis* Meinsch., *C. lenticularis* Michx., *C. luzulina* Olney, *C. nebrascensis* Dewey, *C. pachystachya* Cham. ex Steud., *C. pellita* Muhl. ex Willd., *C. subfusca* W. Boott, *Deschampsia cespitosa* (L.) P. Beauv., *Dodecatheon redolens* (H. M. Hall) H. J. Thoms., *Drosera rotundifolia* L., *Eriophorum angustifolium* Honck., *Hypericum anagalloides* Cham. & Schltld., *Juncus balticus* Willd. subsp. *ater* (Rydb.) Snogerup, *J. covillei* Piper, *J. ensifolius* Wikstr., *J. howellii* F. J. Herm., *J. laccatus* Zika, *J. mertensianus* Bong., *J. nevadensis* S. Watson, *Mimulus guttatus* Fisch. ex DC., *M. primuloides* Benth., *Montia fontana* L., *Narthecium californicum* Baker, *Pedicularis groenlandica* Retz., *Picea engelmannii* Parry ex Engelm., *Pinus contorta* Douglas ex Loudon, *P. jeffreyi* Balf., *P. ponderosa* P. Lawson & C. Lawson, *Salix commutata* Bebb, *S. orestera* C. K. Schneid., *S. pedicellaris* Pursh, *S. planifolia* Pursh, *Scirpus microcarpus* J. Presl & C. Presl, *Senecio triangularis* Hook., *Triantha occidentalis* (S. Watson) R. R. Gates, *Trifolium monanthum* A. Gray, and *Tsuga mertensiana* (Bong.) Carrière.

2A. ***Luzula comosa* var. *comosa***: *Acer circinatum* Pursh, *Alnus rubra* Bong., *Anaphalis margaritacea* (L.) Benth. & Hook. f., *Anthoxanthum odoratum* L., *Aruncus dioicus* (Walter) Fernald, *Carex harfordii* Mack., *C. obnupta* L. H. Bailey, *Deschampsia cespitosa*, *Holcus lanatus* L., *Juncus hesperius* (Piper) Lint, *J. phaeocephalus* Engelm.,

Oenanthe sarmentosa C. Presl ex DC., *Pinus contorta*, *Polystichum munitum* (Kaulf.) C. Presl, *Pseudotsuga menziesii* (Mirb.) Franco, *Pteridium aquilinum* (L.) Kuhn, *Rubus parviflorus* Nutt., and *Sisyrinchium californicum* (Ker Gawl.) Dryand.

2B. ***Luzula comosa* var. *laxa***: *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., *A. grandis* (Douglas ex D. Don) Lindl., *A. magnifica*, *A. procera* Rehder, *Acer circinatum*, *A. macrophyllum* Pursh, *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem., *Arbutus menziesii* Pursh, *Asarum caudatum* Lindl., *Calamagrostis rubescens* Buckley, *Carex abrupta* Mack., *C. brainerdii* Mack., *C. concinnoides* Mack., *C. feta*, *C. fracta* Mack., *C. geyeri* Boott, *C. heteroneura* W. Boott, *C. inops* L. H. Bailey, *C. pachystachya*, *C. rossii* Boott, *C. whitneyi* Olney, *Clintonia uniflora* (Menzies ex Schult.) Kunth, *Corylus cornuta* Marshall, *Fragaria virginiana* Mill., *Holodiscus discolor* (Pursh) Maxim., *Juncus balticus*, *J. hesperius*, *J. patens* E. Mey., *J. tenuis* Willd., *Linnaea borealis* L., *Luzula parviflora* (Ehrh.) Desv., *Physocarpus malvaceus* (Greene) Kuntze, *Picea glauca* (Moench) Voss, *Pinus contorta*, *P. jeffreyi*, *P. monticola* Douglas ex D. Don, *P. ponderosa*, *Polystichum munitum*, *Populus tremuloides* Michx., *Prunus emarginata* (Douglas ex Hook.) Eaton, *Pseudotsuga menziesii*, *Pteridium aquilinum*, *Quercus garryana* Douglas ex Hook., *Q. kelloggii* Newb., *Thuja plicata* Donn ex D. Don, *Toxicodendron diversilobum* (Torr. & A. Gray) Greene, *Trillium ovatum* Pursh, *Tsuga heterophylla* (Raf.) Sarg., and *T. mertensiana*.

3. ***Luzula macrantha***: *Acer macrophyllum*, *Allium acuminatum* Hook., *Arbutus menziesii*, *Arctostaphylos glauca* Lindl., *A. viscida* Parry, *Calochortus monophyllus* (Lindl.) Lem., *Camassia quamash* (Pursh) Greene, *Carex hendersonii* L. H. Bailey, *C. inops*, *C. leptopoda* Mack., *C. multicaulis* L. H. Bailey, *Ceanothus cuneatus* (Hook.) Nutt., *C. pumilus* Greene, *Clarkia gracilis* (Piper) A. Nelson & J. F. Macbr., *Danthonia californica* Bol., *Eriophyllum lanatum* (Pursh) J. Forbes, *Melica torreyana* Scribn., *Pinus jeffreyi*, *P. ponderosa*, *P. radiata* D. Don, *P. sabiniana* Douglas ex D. Don, *Pseudotsuga menziesii*, *Quercus agrifolia* Née, *Q. chrysolepis* Liebm., *Q. douglasii* Hook. & Arn., *Q. garryana*, *Q. kelloggii*, *Q. wislizeni* A. DC., *Ranunculus occidentalis* Nutt., *Rosa nutkana* C. Presl, *Rubus ursinus* Cham. & Schldtl., *Selaginella wallacei* Hieron., *Toxicodendron diversilobum*, *Viola adunca* Sm., *V. purpurea* Kellogg, and *Zygadenus venenosus* S. Watson.

4. ***Luzula subsessilis***: *Ammophila arenaria* (L.) Link, *Anthoxanthum odoratum*, *Arctostaphylos insularis* Greene ex Parry, *Artemisia californica* Less., *Calochortus tolmiei* Hook. & Arn., *Camassia leichtlinii* (Baker) S. Watson, *C. quamash*, *Carex inops*, *C. tumulicola* Mack., *Danthonia californica*, *Erigeron glaucus* Ker Gawl., *Eriophyllum staechadifolium* Lag., *Fragaria chiloensis* (L.) Duchesne, *Fraxinus latifolia* Benth., *Iris douglasiana* Herb., *I. tenax* Dougl. ex Lindl., *Juncus occidentalis* (Coville) Wiegand, *Leymus mollis* (Trin.) Pilg., *Lomatium utriculatum* (Nutt. ex Torr. & A. Gray) J. M. Coult. & Rose, *Lupinus littoralis* Douglas ex Lindl., *Melica californica* Scribn., *Mimulus aurantiacus* Curtis, *Pinus contorta*, *P. muricata* D. Don, *P. radiata*, *P. torreyana* Parry ex Carrière, *Potentilla gracilis* Douglas ex Hook., *Pseudotsuga menziesii*, *Quercus chrysolepis*, *Q. dumosa* Nutt., *Q. garryana*, *Q. kelloggii*, *Q. pacifica* Nixon & C. H. Mull., *Q. tomentella* Engelm., *Q. wislizeni*, *Ranunculus californicus* Benth., *Rubus ursinus*, *Salix hookeriana* Barratt ex Hook., *Selaginella bigelovii* Underw., *Toxicodendron diversilobum*, *Viola adunca*, and *V. pedunculata* Torr. & A. Gray.