**SPECIES: Chondrilla juncea**

Choose from the following categories of information.

- Introductory
- Distribution and occurrence
- Botanical and ecological characteristics
- Fire ecology
- Fire effects
- Management considerations
- References

**INTRODUCTORY**

**SPECIES: Chondrilla juncea**

- **AUTHORSHIP AND CITATION:**

- **FEIS ABBREVIATION:**
  CHOJUN

- **SYNONYMS:**
  None

- **NRCS PLANT CODE [94]:**
  CHJU

- **COMMON NAMES:**
  rush skeletonweed
  hognibble
  nakedweed
  skeletonweed

- **TAXONOMY:**
  The currently accepted name for rush skeletonweed is *Chondrilla juncea* (Asteraceae) [18, 34, 45, 46, 48, 89, 96, 103].
LIFE FORM:
Forb

FEDERAL LEGAL STATUS:
No special status

OTHER STATUS:
At the time of this writing (2003) rush skeletonweed is listed as a regulated or noxious weed or weed seed in at least 9 U.S. states and 1 Canadian province. See the Plants, Invaders, or APHIS databases for more information.

DISTRIBUTION AND OCCURRENCE

SPECIES: Chondrilla juncea

- GENERAL DISTRIBUTION
- ECOSYSTEMS
- STATES/PROVINCES
- BLM PHYSIOGRAPHIC REGIONS
- KUCHLER PLANT ASSOCIATIONS
- SAF COVER TYPES
- SRM (RANGELAND) COVER TYPES
- HABITAT TYPES AND PLANT COMMUNITIES

GENERAL DISTRIBUTION:
According to several reviews [19,58,67], rush skeletonweed is thought to have originated in the submontane region surrounding the Caspian Sea, where the genus Chondrilla is most diverse. From there it spread to the Mediterranean region and central Europe. Its "native range" extends from western Europe and north Africa to central Asia [58].

Rush skeletonweed was first reported in Australia in 1918. The heaviest infestations were initially in the cereal growing area of New South Wales and Victoria, and later spread into western Australia [67].

Rush skeletonweed was apparently introduced to North America in contaminated plant material, contaminated seed, or with animal fodder or bedding [71]. Rush skeletonweed established in eastern North America around 1872. It occurs in Ontario, Michigan, Indiana, and from New York to Virginia [48]. It is reported from 1 county in Georgia [94]. Rush skeletonweed was first reported in Washington in 1938, but may have established as long as 30 years prior to that report [63]. It was first reported in California in 1965 [58,63]. Over time it has become widespread and locally dense in rangelands, wheat growing areas, and along transportation corridors, in parts of California, Oregon, Washington, Idaho, Montana, and British Columbia [18,30,58,74,80]. Estimates of the extent of rush skeletonweed infestation in North America range from 6.2 million acres (2.5 million ha) of rangeland in the Pacific Northwest and California [53], to around 8.4 million acres (3.4 million ha) of crop and rangeland in the U.S. [40]. State distribution of rush skeletonweed in the United States can also be viewed at Plants database.

The following lists include North American ecosystems, habitats, and forest and range cover types in which rush skeletonweed is known or thought to be invasive, as well as some that may be invaded by rush skeletonweed following disturbances in which vegetation is killed and/or removed and/or soil disturbed (e.g.
cultivation, logging, fire, grazing, herbicide application, flooding). These lists are not necessarily exhaustive. More information is needed regarding incidents and examples of particular ecosystems and plant communities where rush skeletonweed is invasive.

**ECOSYSTEMS [33]**:
FRES10 White-red-jack pine
FRES14 Oak-pine
FRES15 Oak-hickory
FRES20 Douglas-fir
FRES21 Ponderosa pine
FRES22 Western white pine
FRES28 Western hardwoods
FRES29 Sagebrush
FRES34 Chaparral-mountain shrub
FRES35 Pinyon-juniper
FRES36 Mountain grasslands
FRES37 Mountain meadows
FRES42 Annual grasslands

**STATES/PROVINCES:** (key to state/province abbreviations)

**UNITED STATES**

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**CANADA**

| BC | ON |

**BLM PHYSIOGRAPHIC REGIONS [9]**:
1 Northern Pacific Border
3 Southern Pacific Border
4 Sierra Mountains
5 Columbia Plateau
8 Northern Rocky Mountains

**KUCHLER [49] PLANT ASSOCIATIONS:**
K002 Cedar-hemlock-Douglas-fir forest
K010 Ponderosa shrub forest
K011 Western ponderosa forest
K012 Douglas-fir forest
K013 Cedar-hemlock-pine forest
K024 Juniper steppe woodland
K026 Oregon oakwoods
K028 Mosaic of K002 and K026
K030 California oakwoods
K038 Great Basin sagebrush
K048 California steppe
K050 Fescue-wheatgrass
K051 Wheatgrass-bluegrass
K055 Sagebrush steppe
K056 Wheatgrass-needlegrass shrubsteppe
K063 Foothills prairie

SAF COVER TYPES [32]:
210 Interior Douglas-fir
220 Rocky Mountain juniper
227 Western redcedar-western hemlock
233 Oregon white oak
234 Douglas-fir-tanoak-Pacific madrone
237 Interior ponderosa pine
238 Western juniper
250 Blue oak-foothills pine

SRM (RANGELAND) COVER TYPES [86]:
101 Bluebunch wheatgrass
102 Idaho fescue
103 Green fescue
104 Antelope bitterbrush-bluebunch wheatgrass
105 Antelope bitterbrush-Idaho fescue
106 Bluegrass scabland
107 Western juniper/big sagebrush/bluebunch wheatgrass
109 Ponderosa pine shrubland
110 Ponderosa pine-grassland
201 Blue oak woodland
214 Coastal prairie
215 Valley grassland
302 Bluebunch wheatgrass-Sandberg bluegrass
304 Idaho fescue-bluebunch wheatgrass
305 Idaho fescue-Richardson needlegrass
309 Idaho fescue-western wheatgrass
311 Rough fescue-bluebunch wheatgrass
312 Rough fescue-Idaho fescue
314 Big sagebrush-bluebunch wheatgrass
315 Big sagebrush-Idaho fescue
316 Big sagebrush-rough fescue
322 Curlleaf mountain-mahogany-bluebunch wheatgrass
401 Basin big sagebrush
402 Mountain big sagebrush
403 Wyoming big sagebrush
404 Threetip sagebrush
407 Stiff sagebrush
409 Tall forb
412 Juniper-pinyon woodland
420 Snowbrush

HABITAT TYPES AND PLANT COMMUNITIES:
A review by McVean [58] reports several plant associations in which rush skeletonweed occurs in Eurasia. Rush skeletonweed is characteristic of needlegrass-sagebrush (Achnatherum/Stipa-Artemisia) steppe in Russia, Iraq, Anatolia and eastern Europe. It occurs in a variety of open, "semi-natural" communities in the Mediterranean region and in the upper oak scrubs of Kurdistan and Khalifan in Iraq. It is recorded as a constituent of "thin pine forests" on sandy soils in part of Russia. Rush skeletonweed is recorded on Mt. Ararat along with gray rockcress (Arabis caucasica), Juniperus oxycedrus, and puncturevine (Tribulus terrestris);
and occurs in *Stipa szovitsiana* steppe in the same region ([58] and references therein). Plants associated with rush skeletonweed in Greece include Bermuda grass (*Cynodon dactylon*), wheat (*Triticum* spp.), corn chamomile (*Anthemis arvensis*), and corn poppy (*Papaver rhoas*), with field eryngo (*Eryngium campestre*), and yellow starthistle (*Centaurea solstitialis*) among the most frequently encountered associates [98]. The most common plants co-occurring with rush skeletonweed on degraded coastal dune sites in southern France were Bermuda grass, thinleaf false brome (*Brachypodium phoenicoides*), leafybract dwarf rush (*Juncus capitatus*), onionweed (*Asphodelus fistulosus*), and strawflower (*Helichrysum stoechas*) [99].

In Australia, rush skeletonweed is essentially a weed of cultivation and of open areas with disturbed soils. In general the plants most frequently associated with rush skeletonweed in Australia are the numerous weeds and other plants found in cereal crops and pastures. In pastures, there is often an inverse relationship between density of rush skeletonweed and that of legumes such as subterranean clover (*Trifolium subterraneum*), annual medics (*Medicago* spp.), and alfalfa (*Medicago sativa*). Hellroot (*Orobanche minor*) often occurs as a parasite on rush skeletonweed in subterranean clover stands ([67] and references therein). Rush skeletonweed has seldom succeeded in invading native vegetation in Australia except where native vegetation has been weakened by drought and/or overgrazing. Rush skeletonweed has been recorded as a constituent of eucalyptus (*Eucalyptus* spp.) savanna woodland and of "rough pasture" derived from eucalyptus communities, along with several other plants including Russian-thistle (*Salsola kali*). It is also considered "naturalized" in some needlegrass grasslands ([58] and references therein). McVean [58] provides additional lists of native and nonnative plants that occur in areas where rush skeletonweed may be found in Australia.

Descriptions of North American habitats in which rush skeletonweed occurs are limited. Old [62,63] provides a detailed account of habitat types and plant associations with which rush skeletonweed is associated in Washington, although he qualifies his information by pointing out that these classifications are of little predictive value due to massive disturbances. Rush skeletonweed occurs in bluebunch wheatgrass-Sandberg bluegrass (*Pseudoroegneria spicata-Poa secunda*) and stiff sagebrush (*Artemisia rigida*)-Sandberg bluegrass habitat types that occur on the channeled scablands of eastern Washington. Rush skeletonweed is also common on the sandy to gravelly soils of the glacial lobes (see Site Characteristics), which are characterized by an association of ponderosa pine (*Pinus ponderosa*) and common snowberry (*Symphoricarpos albus*) which shifts to Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) at higher elevations. Grazing, trampling, cultivation, logging, and burning have modified these environments such that nonnative plants are often better indicators of site potential than are native plants. Dalmatian toadflax (*Linaria dalmatica*) is a prime indicator of rush skeletonweed sites in the glacial lobes, and wavyleaf thistle (*Cirsium undulatum*) is a key indictor of rush skeletonweed habitats in the channeled scablands [62].

The plant species recorded in association with rush skeletonweed in Washington can be divided into 4 categories as follows [62,63]:

1. Species known to have an extremely wide ecologic amplitude, such as cheatgrass (*Bromus tectorum*), goatsbeard (*Tragopogon* spp.), western yarrow (*Achillea millefolium*), prickly lettuce (*Lactuca serriola*), tumblemustard (*Sisymbrium altissimum*), alfalfa, sweetclover (*Melilotus* spp.), and quackgrass (*Elytrigia repens*).
2. Species generally found on sites of low effective precipitation but not uncommon on other sites, such as velvet lupine (*Lupinus leucophyllus*), tall annual willowherb (*Epilobium brachycarpum*), tarweed (*Madia* spp.), Canadian horseweed (*Conyza canadensis*), common St. Johnswort (*Hypericum perforatum*), winter vetch (*Vicia villosa*), trefoil (*Lotus* spp.), sheep sorrel (*Rumex acetosella*), soft chess (*Bromus hordeaceus*), common mullein (*Verbascum thapsus*), and fleabane (*Erigeron* spp.).
3. Species restricted to sites of low effective precipitation such as bottlebrush squirreltail (*Elymus elymoides*), snow buckwheat (*Eriogonum niveum*), woolly plantain (*Plantago patagonica*), field cottonrose (*Logfia arvensis*), varieaf phacelia (*Phacelia heterophylla*), large knotweed (*Polygonum douglasii* spp. *majus*), and bluebunch wheatgrass.
4. Species restricted to sites of low effective precipitation and generally restricted to a specific habitat (e.g. channeled scablands and Spokane glacial lobe), such as cutleaf daisy (*Erigeron compositus*), Nevada bird's-foot trefoil (*Lotus nevadensis*), wavyleaf thistle, and Dalmatian toadflax.

In Canada, rush skeletonweed occurs, and could potentially spread widely, in disturbed and open-canopied sites in the interior Douglas-fir ecozone of British Columbia [40]. The predicted distribution in Canada includes the rough fescue (*Festuca altaica*) and montane ecozones in Alberta, the drier parts of the interior cedar-hemlock (*Thuja-Tsuga*) ecozone in the interior of British Columbia, the Douglas-fir-shore pine (*Pinus contorta* var. *contorta*-)madrone (*Arbutus* spp.) site association in southwestern British Columbia, and parts of southern Vancouver Island [40]. At Vernon, British Columbia, rush skeletonweed occurs on a degraded grassland site where sulphur cinquefoil (*Potentilla recta*) dominates [56].

### BOTANICAL AND ECOLOGICAL CHARACTERISTICS

**SPECIES: Chondrilla juncea**

- **GENERAL BOTANICAL CHARACTERISTICS**
- **RAUNKIAER LIFE FORM**
- **REGENERATION PROCESSES**
- **SITE CHARACTERISTICS**
- **SUCCESSIONAL STATUS**
- **SEASONAL DEVELOPMENT**

**GENERAL BOTANICAL CHARACTERISTICS:**
Correct identification of rush skeletonweed is important, especially if control strategies are planned. Identification can be difficult, especially in the vegetative state, as rush skeletonweed rosettes resemble a number of other plants that possess rosettes of lobed or dentate leaves, such as catsear (*Hypochaeris* spp.), distaff thistle (*Carthamus* spp.), hawksbeard (*Crepis* spp.), hawkbit (*Leontodon* spp.), dandelion (*Taraxacum* spp.), lettuce (*Lactuca* spp.), agoseris (*Agoseris* spp.), and various mustards (Brassicaceae) ([63,67] and references therein). Rush skeletonweed can be distinguished from most of these by considering in combination the following: a) rush skeletonweed leaves are glabrous, b) rush skeletonweed leaf lobes project backward, as a barbed spear, and c) rush skeletonweed exudes latex from cut or broken surfaces [62,67,82]. Additionally, the long thin taproot of rush skeletonweed is distinctive. A rush skeletonweed seedling of only a few inches width may have a root up to 14 inches (36 cm) long, while most other easily confused genera have a short, stout taproot. Leaf color may also be used as a discriminating character. Rush skeletonweed leaves on at least some plants show tinges of reddish-brown and are in general darker than other genera [62,63]. Flowering rush skeletonweed plants are distinctive with their tall, usually leafless, highly branched flowering stems that produce flat capitula with yellow flowers in summer and autumn, and dark brown bristles near the base of the stem [63,67].

Rush skeletonweed should also not be confused with rush skeletonplant (*Lygodesmia juncea*), which is native in many parts of North America. Rush skeletonplant does have latex, but lacks a winter rosette, grows only 4 to 16 inches (10-40 cm) tall, and has pink (rarely white) flowers [40].

The following description of rush skeletonweed provides characteristics that may be relevant to fire ecology, and is not meant for identification. Keys for identification are available (e.g. [18,34,45,46,96,103]).

**Morphology:**
Rush skeletonweed is a deep-rooted forb, mostly 16 to 60 inches (40-150 cm) tall, somewhat rush-like in
Species: Chondrilla juncea  
http://www.fs.fed.us/database/feis/plants/forb/chojun/all.html

appearance. Rush skeletonweed basal leaves are well developed, 2 to 5 inches (4-13 cm) long and 0.6 to 1.8 inches (15-45 mm) wide, forming a rosette that is often deciduous at flowering. Each rush skeletonweed rosette produces 1 flowering stem, with multiple spreading or ascending branches. Stem leaves are lacking in some plants and when present are reduced, linear, 0.8 to 4 inches (2-10 cm) long and 0.04 to 0.3 inches (1-8 mm) wide. Stem leaves are also often deciduous, and upper leaves are often reduced to scale-like bracts. Flowerheads are produced along or at the ends of stems, either individually or in groups of 2 to 5, each with 9 to 12 flowers. The involucre is 0.4 to 0.5 inch (9-12 mm) high. Rush skeletonweed fruits are achenes (referred to subsequently as seeds), about 0.1 inch (3 mm) long, with a slender beak at the top, bearing a copious pappus of numerous capillary bristles, 0.2 inch (5-6 mm) long. The leaf, stem, and roots of rush skeletonweed exude a milky latex when cut or broken [18, 34, 45, 46, 58, 60, 67, 89, 96].

Root system:  
Rush skeletonweed has a slender, simple taproot, that can reach over 6.5 feet (2 m) deep and branch at depth into C-horizon soil and fissures in bedrock. This root system provides rush skeletonweed with access to a large volume of soil and to potentially large reserves of soil-stored water [58, 60, 67]. In Central Europe, a rush skeletonweed plant was found with a well-developed taproot penetrating to a depth of almost 8 feet (2.3 m). This root forked repeatedly in its lower half, but had little lateral extension (Kutchera 1960 as cited by [58, 80]). In very sandy or gravelly soils, and in waterlogged soils, lateral roots are often formed [58, 60]. On the upper part of the primary root or on larger lateral roots near the soil surface, buds may be formed which produce daughter rosettes in undisturbed plants [23, 67, 80]. All parts of the root system, especially deeper parts, are brittle and easily broken (Kutchera 1960 as cited by [58, 80]), and new plants can arise from root fragments (see Asexual regeneration). Roots of rush skeletonweed may be colonized by vesicular arbuscular mycorrhizae fungi [39].

Variation: Rush skeletonweed is an apomict, reproducing without pollination or genetic recombination (see Breeding system). Therefore a particular gene combination can be expected to be maintained in the short term, as seedlings and daughter plants are genetically identical to their parent (clones) ([67] and references therein). Over long periods, new variants may arise through autosegregation and/or random mutation as is evidenced by the high amount of clonal variation in rush skeletonweed in its native range [16]. Populations are typically composed of more than 1 genotype, although the level of diversity is usually substantially less than that in the western part of Turkey where sexual diploid populations can also occur ([16] and references therein).

In Australia, 3 morphologically distinct "forms" (A, B, and C) or types of rush skeletonweed have been identified and can be distinguished by shape of rosette leaves, inflorescence morphology, fruit characters and regenerative potential from root fragments ([67] and references therein). Later work revealed that these types can be differentiated by isozyme patterns of 5 enzyme systems [12]. Chaboudez [16] found no match between clones in Australia (3 clones from 23 populations) and clones in Turkey (91 clones from 123 sites) using isozyme analysis.

Accounts of variation in North American populations are unclear and inconsistent. In Washington, Rosenthal and others [80] identified 2 distinct types of rush skeletonweed. One type is an upright branching plant that grows to a maximum height of 33 inches (85 cm), and the other is more flatly branched and attains a maximum height of 16 inches (40 cm). The shorter type begins flowering from mid-June to July, and the taller type begins flowering 15 to 30 days later [80]. According to Piper [72], the early-flowering type can grow to 24 inches (60 cm) tall, and is bushier and more compact in appearance than the late-flowering type. The late-flowering type has stems that are thicker, more erect and may grow as tall as 47 inches (120 cm). Both types frequently inhabit the same areas, although the late-flowering type is more numerous and widely distributed [72]. According to Harris [40] 3 distinct types of rush skeletonweed occur in the Pacific Northwest. Two of these grow to 51 inches (130 cm) tall and differ by flowering start (July or August). The 3rd type grows 26 to 35 inches (65-90 cm) tall, is highly branched, and begins flowering mid-July [40]. These 3 types have distinct and stable isozyme patterns [41]. Chaboudez [16] also states that 3 triploid clones have been identified in the U.S. No attempt has been made to name and publish any of these types as separate taxa at the
subspecific level [63]. Old [63] suggests the possibility that many unrecognized varieties of rush skeletonweed may exist in North America.

**Life span:**
Little information is available on the longevity of either disturbed or undisturbed rush skeletonweed plants [58]. The life span of individual plants varies, being determined by the interactive effects of such factors as drought, mechanical and chemical treatments, competition from other species and, for at least 1 type, attack by biological control agents [67]. Often described as a biennial or short-lived perennial in its native range, rush skeletonweed is described as a relatively long-lived perennial in Australia, especially where it is subjected to repeated disturbance and damage [58,60]. According to Harris [40] rush skeletonweed plants live 3-4 years in Eurasia, but over 20 years in Australia.

**Stand structure:**
Under favorable conditions, rush skeletonweed populations may develop extremely high densities. Rosette densities of up to 500 rush skeletonweed plants per m² were recorded on sandy soils in Victoria, Australia (Wells 1969, as cited by [67]). Rush skeletonweed stem densities of up to 20 to 60 stems per m² are recorded in summer-dry montane and Mediterranean habitats on crop and rangeland sites in the western U.S. [40].

**RAUNKIAER [77] LIFE FORM:**
Hemicryptophyte
Geophyte

**REGENERATION PROCESSES:**
Rush skeletonweed reproduces by seed, by root fragments, and by vegetative spread from vertical and lateral roots.

**Breeding system:** Rush skeletonweed is triploid and exhibits obligate apomyxis ([24,58] and references therein), although sexual diploid populations can occur in the western part of Turkey ([16] and references therein). This breeding system may be beneficial to an invasive species in that it promotes genetic stability and also enables plants to reproduce in areas where environmental factors or pollinators may be limiting (Duke 1985, as cited by [54]).

**Pollination:** Experimental evidence presented by McVean [58] and Cuthbertson [24] indicates that viable seed production in rush skeletonweed is completely independent of pollination. Flowers are visited by a wide variety of insects, and bees are known to collect the pollen; however, these insects serve no function for the plant [40,58].

**Seed production:** Rush skeletonweed seed production is extremely variable [19]. Rush skeletonweed plants can produce large amounts of seed over a relatively long period. Potential seed production has been estimated in the order of 70,000 seeds per m² in a dense infestation in Australia (Cuthbertson 1967, as cited by [67]). Seed production and viability are determined primarily by the vigor of the plant up to the point of seed maturity [19], and may depend on plant age, plant genotype, moisture availability, summer air temperatures, infection with biological control insects, interactions with other control methods, and other site management factors.

Rush skeletonweed flowerheads develop singly or in clusters of 2 to 5. Each head produces 9 to 12 florets, each floret forms a seed, and viability is generally high [24,54]. Most Australian first-year rush skeletonweed plants grown in a greenhouse produced between 59 and 150 flowerheads, with 10 to 12 flowers per head, and total seed production between 500 and 1,500 seeds per plant [58]. McVean [58] predicted that older, multiple-stemmed plants growing under field conditions could produce 10 times as many seeds.
In western Australia, rush skeletonweed plants (types A and C) grown in a greenhouse produced between 3,000 and 13,070 seeds per plant, with 82% viability on average. Total number of seeds in rush skeletonweed plants grown in agricultural fields ranged from 13,730 to 27,550 and averaged 19,926 seeds per plant, with 75% viability. Some plants less than 1 year old produced more than 10,000 seeds in the field [67].

Seed production characteristics also differed between the 2 types tested. At one site, type C plants produced significantly (p<0.001) more seed (14,120 vs. 8,430 seeds per plant), of greater viability (79.4% vs. 73.9%), and with lower primary seed dormancy (3.5% vs. 11%), with less variation between harvest dates than type A plants [28].

According to Cuthbertson [24] and McVean [58], moisture availability during flowering and seed maturation is a major factor in determining reproductive capacity in rush skeletonweed. McVean [58] found that well-watered plants produced seeds containing greater than 90% fully developed embryos, whereas droughted plants produced fewer than 10% viable seed. Under the most severe drought, flowering failed altogether. Similarly, Dodd and Panetta [28] found that simulated drought reduced seed numbers, viability, primary dormancy and seed weight in greenhouse-grown rush skeletonweed plants, although the 2 types, A and C, responded differently. Type A control plants averaged 7,570 seeds per plant one year and 8,290 seeds per plant the following year when type C control plants produced 2,750 seeds per plant. Drought reduced total seed numbers by 75% in type A plants, and by 46% in type C plants [28].

Conversely, in field experiments in western Australia, most field-grown plants (types A and C) produced abundant viable seed, even without substantial summer rainfall. Summer rain did not increase seed output or affect viability in established plants, and there were no relationships in either type between the various seed characteristics and cumulative rainfall for different 2-week periods prior to seed harvest. According to Panetta and Dodd [67], rush skeletonweed's extensive root system allows it to "become largely independent of" summer rainfall for flower and seed production. However, long-term drought retards growth and development of rush skeletonweed, and limits production of viable seeds [67,100].

Rush skeletonweed seed production and viability appear to be sensitive to high summer temperatures (daytime maxima exceeding 91 °F (33 °C)) with low air humidity and low soil moisture [58]. Exceptionally high air temperatures appeared to depress seed numbers and/or viability at several sites [28].

Activity of biological control agents can also affect viable seed production in rush skeletonweed (see [Biological control]). A large difference in rush skeletonweed seed production was observed between 2 sites near Canberra, Australia, with seed output at one site at 4 seeds per m² compared with 1,642 seeds per m² at another site. The only difference between the 2 areas was the presence of 3 biological control organisms (the rust, the mite, and the midge) at the former site [19]. Stem colonization by gall mites (Eriophyes chondrillae) reduces the number of flowers and seeds produced. In greenhouse experiments, rush skeletonweed plants without gall mites averaged 57 floral stems per plant, and the number of floral stems per plant decreased with increasing mite density. Plants averaging 180 mites per plant had 27 flowering stems; plants averaging 890 mites per plant had 18 flowering stems; and plants averaging 1600 mites per plant had 15 flowering stems [73]. In Washington, McLellan [57] observed reduced seed production in gall mite-infested rush skeletonweed plants compared with uninfested plants; and Cullen and others [20] demonstrated up to 96% reduction in flower production in rush skeletonweed plants infected by gall mites.

Mowing rush skeletonweed before flowering, once or twice in a season, resulted in significantly (p<0.05) lower seed production [57].

**Seed dispersal:** Rush skeletonweed seeds are readily dispersed. Seeds are small and possess both a pappus, which facilitates wind dispersal, and a rough seed coat with small teeth, which increases the chances of attachment to animals and other vectors. Rush skeletonweed seed may also be dispersed by a variety of human vectors, including
rush skeletonweed contamination of agricultural products, especially hay. Transportation corridors are a common location for rush skeletonweed seed dispersal [67].

Seed banking:
According to several researchers, rush skeletonweed seeds remain viable for several years in the laboratory. Cuthbertson [22] found that germination rates remain high (93.6% to 98.7%) for rush skeletonweed seed stored in open containers in the laboratory for 1 to 2 years. Germination rates decreased rapidly after that, with some germination after 3 years, 0% to 2.6% germination after 4 years, and no germination after 5 years of storage. Storage temperature and other conditions are not given [22]. According to Old [62] rush skeletonweed seeds refrigerated at 37 °F (3 °C) maintained a high degree of viability for up to 8 years and showed a low degree of viability after as long as 16 years. In most cases length of time to germinate increased with length of storage. Liao and others [53, 54] found that up to 60% of rush skeletonweed seeds collected in Idaho remained viable after 1 year of storage, with viability decreasing over time. Stored seeds generally exhibited higher germination rates (90% average) than fresh seeds (67% average), indicating possible dormancy and afterripening effects [53].

Several authors suggest that most rush skeletonweed seeds exhibit little or no dormancy (estimates between 0 and 40% dormancy) [22, 58, 60, 65, 82], although this attribute appears to vary between rush skeletonweed types [67]. Because mature rush skeletonweed seeds typically germinate readily, regardless of collection date, over a wide range of temperatures, and independent of light availability [53, 58, 64], they may not form a long-lived seed bank. Further evidence to support this comes from studies indicating that rush skeletonweed seeds are short-lived under field conditions and generally survive for less than 6 to 18 months [64, 82]. Liao and others [53] found up to 60% of non-germinating rush skeletonweed seeds were viable, suggesting that nongerminating seeds may persist in the seedbank under some conditions.

Panetta [64] found that buried rush skeletonweed seeds germinated readily following summer rainfall events of less than 0.4 inch (10 mm) in Australia. Seedlings did not survive due to inadequate moisture availability following germination. Seeds lying on the surface were less likely to germinate in response to small rainfall events, but were prone to predation by seed-harvesting ants. These conditions lead to considerable losses of rush skeletonweed seed. Panetta [64] also found that only "a few" rush skeletonweed seeds survived after 4 months burial at 2 inches (4 cm). According to Cullen and Groves [19], fire and breakdown by pathogens may also lead to rush skeletonweed seed losses, although no details are given.

There is little to no rush skeletonweed seed accumulation between years under field conditions [19, 58, 65]. Panetta [65] measured a maximum of 3.1% of a rush skeletonweed seed crop surviving between years, during a year with a particularly dry summer. In Washington, attempts to recover rush skeletonweed seeds from soil under dense infestations have been unsuccessful, a factor which gives some support to the Australian conclusion that few rush skeletonweed seeds remain viable in the field from one year to the next [82].

Germination:
In general, rush skeletonweed seeds have high viability and high germination rates. Viability is not dependent on pollinators [24] and does not appear to be affected by moisture availability during the growing season [54], although it does appear to decrease during storage [22, 54, 60, 62]. Germination of rush skeletonweed seeds does not require light [22, 58] and occurs over a wide range of temperatures [58, 60]. Germination is sensitive to moisture availability and depth of seed burial [22].

Cuthbertson [24] found 95.8% seed viability from unstressed rush skeletonweed plants, while McVean [58] found that, even under ideal germination conditions, up to 20% of ripe embryos may "remain dormant or die." Normally dispersed rush skeletonweed seeds collected in Washington gave no indication of innate dormancy. Immediately after collection, samples gave 95% germination on blotters [82]. Storage tests indicate viability may be lost over time (see Seed banking).
Rush skeletonweed seeds from 2 populations of rush skeletonweed in southwestern Idaho were capable of immediate germination without scarification or wet prechilling. Total germination generally ranged from 60 to 100% throughout the entire seed production period (July through October). Germination percentages were lower for rush skeletonweed seeds harvested late in the season. Germination was rapid, reaching 50% of total in less than 12 days. Germination differed among harvest dates, rearing sites, and between years of collection. Rush skeletonweed seed from the lower elevation site tended to have higher viability, especially early in the season. Seeds formed in the dry year (4%-33% below average precipitation) were as viable and had higher and faster germination than those from the wet year (12%-43% above average precipitation) [53,54].

Rush skeletonweed seed germination occurs over a wide range of temperatures between 45 and 104 °F (7-40°C) [58,60]. Germination is extremely rapid at the optimum temperature (around 77 °F (25 °C)), beginning within 6 to 8 hours and reaching 60% to 90% of its maximum within 24 hours [58]. Germination of rush skeletonweed seed was higher at an incubation temperature regime of 68/50 °F (20/10 °C) (50% germination in 6 days) as compared with 68/86 °F (20/30 °C) (50% germination in 9.5 days) (dark/light, respectively) [53].

Germination of rush skeletonweed seed is sensitive to moisture availability. Cuthbertson [22] found that rates and final percentages of germination were reduced progressively at osmotic tensions below -0.2 MPa, until germination ceased at -1.6 MPa. According to Schirman and Robocker [82], water held by the pappus of a group of rush skeletonweed seeds following a summer shower in Washington is sufficient to support radicle elongation. They found complete germination inhibition only at tensions exceeding -1.5 MPa [82]. Similarly, buried rush skeletonweed seeds germinated readily following summer rainfall events of less than 0.4 inch (10 mm) in Australia [64].

Moisture loss may be rapid when fully or partially imbibed rush skeletonweed seeds are exposed to drying influences, so germination may be promoted by slight burial [58,67]. In Australian studies, rush skeletonweed seeds lying on the surface were much less likely to germinate in response to small rainfall events [64]. Seedlings emerged successfully from rush skeletonweed seeds buried up to about 2 inches (5 cm) in sandy soil, but did not emerge from seeds at this depth in soils of finer texture [58]. Maximum depth of seed burial resulting in rush skeletonweed seedling emergence was 1 inch (2.5 cm) in a medium-textured soil, and no emergence was observed from seeds buried below 0.75 inch (2 cm) in clay soils ([60] and references therein). Rush skeletonweed seeds are sensitive to reduced oxygen and fail to germinate below the surface of waterlogged soil [58].

Seedling establishment/growth:
Rush skeletonweed seedling establishment is highly variable from year to year and from site to site [19], and depends on moisture supply, soil texture and nutrient status, and depth of seed burial.

Rush skeletonweed seedlings require a continuous supply of moisture for 3 to 6 weeks in order to establish a viable root system and to avoid death by desiccation [19]. Depletion of seed pools may follow isolated rainfall during summer months, when there is enough moisture to allow germination, but not enough to support seedling establishment [58,64]. During experiments in Australia, only 0.03% of viable rush skeletonweed seeds established seedlings following 1.5 inches (38 mm) of simulated rainfall during January (summer), whereas 50% establishment occurred under similar conditions in autumn [58]. Panetta [64] observed virtually no establishment from summer germination.

Rush skeletonweed seedling establishment is also dependent on soil conditions. Experimental evidence presented by McVean [58] indicates that soil disturbance is extremely favorable to seedling establishment and must be a factor of considerable importance in the field. Cuthbertson [22] presents data on rush skeletonweed seed germination and seedling establishment in different soil types at varying burial depths. Emergence was reduced and delayed with increased burial depth in all soil types, with little emergence from rush skeletonweed seeds buried deeper than 1 inch (2.5 cm), and no emergence from seeds buried 2 inches (5 cm)
deep in any soil type. Optimum emergence was from a depth of 0.2 inch (6 mm) in all soils except sand. Hypocotyl extension by rush skeletonweed was restricted in clays relative to other soils. Cracking and heaving in clay soils may also impede rush skeletonweed establishment [22].

Survivorship of 1st-year rush skeletonweed plants was higher on a deep sand than on a loamy sand overlaying a sandy clay (duplex soil) in Australia. Mortality on the latter was associated with drying of the A horizon during early summer. No rush skeletonweed plants produced seeds in their 1st year of growth on the duplex soil. Both rush skeletonweed plant types tested produced viable seeds when growing on the deep sand in both years of the study. The author suggests that while large areas of the Australian wheatbelt may be climatically suitable for rush skeletonweed, its invasive potential may be limited by edaphic characteristics over large areas [66].

Experimental evidence presented by McVean [58] indicates fairly high levels of readily available calcium and phosphorus are both important for initial establishment of rush skeletonweed seedlings. Low levels of nitrogen (0.062%) do not preclude rush skeletonweed establishment, although seedlings do better with higher levels. Rush skeletonweed seedlings are also sensitive to competition and shading from other plants [58,82].

Asexual regeneration:
The primary means of local population increase of rush skeletonweed is through vegetative regeneration rather than by seedling establishment [19,67], although this may vary among years. Rush skeletonweed has an extensive and persistent root system and can reproduce vegetatively by adventitious buds on vertical and lateral roots in undisturbed plants, and in response to injury [23].

The taproot of rush skeletonweed may reach several meters into soil and branch at depth. Lateral root production in rush skeletonweed may vary with soil type, plant density, and plant biotype. Lateral roots occur most commonly on rush skeletonweed plants in sandy soils [19], and in sparse stands of rush skeletonweed rather than in dense stands. In Washington, the early-flowering type had more lateral roots than the late-flowering type [80]. Many laterals are short (<3 inches (8 cm) long) and ephemeral, lasting 1 season at most, while some laterals near the soil surface show taproot characteristics and grow horizontally for 6 to 20 inches (15-50 cm) before turning downward [67].

In established, undisturbed rush skeletonweed plants, daughter rosettes can develop from adventitious buds near the top of the tap root, giving rise to a root crown that bears several rosettes with a common root system [23]. These stem buds usually occur in the upper 2 to 4 inches (5-10 cm) of the main taproot [23,80]. Rosettes may also form from buds along the main lateral roots, 3 to 6 inches (8-15 cm) below the soil surface, and about 8 to 18 inches (20-45 cm) away from the parent plant. These rosettes may form their own roots to become satellite plants when the original lateral root connection with the parent plant breaks down [19,23,40,58,62,67,80]. Rush skeletonweed infestations may spread by as much as 2 feet (0.6 m) per year by formation of satellite plants along lateral roots [62].

It appears that the asexual regenerative capacity of rush skeletonweed plants during bolting, flowering and seed production is lower than that of vegetative plants. Rush skeletonweed plants observed in Washington ceased bud production after flower stem initiation in mid-April, and started again after seeds were dispersed in mid-September to early October [80].

When established rush skeletonweed plants are subjected to cutting, grazing, herbicide or insect damage, or any severe injury to rosettes or taproots, adventitious root buds may be produced almost anywhere on the remaining root system and give rise new rosettes [23,37,58,67,73]. New stems can reputedly reach the surface from buds over 3 feet (1 m) deep [58,67], although most regeneration occurs from depths of less than 18 inches (45cm) ([67] and references therein).

A critical factor in rush skeletonweed regeneration after injury is the energy balance of the root [19]. The
relatively thick and fleshy taproot and main branch roots are usually rich in carbohydrate reserves ([23, 67] and references therein). The level of carbohydrate reserves is relative to the age of the plant, time between successive injuries, and the rate of recovery as influenced by vigor of the resulting top growth [19]. Regeneration was observed from 5-week-old plants after removal of the rosette at ground level (Groves and Hull 1966, as cited by [23]). Under field conditions, however, the small roots of such young plants would be extremely susceptible to desiccation and therefore unlikely to regenerate [23].

Rush skeletonweed roots are extremely fragile [60] and when severed, new rush skeletonweed shoots can form from detached root fragments [23, 37, 58, 62, 63, 80]. Cultivation or other soil disturbance can greatly increase rush skeletonweed rosette density since the roots become fragmented and each tiny fragment may give rise to a new plant [37, 58, 62, 63, 98]. The regenerative capacity of rush skeletonweed by root fragments is influenced by moisture availability, fragment size, depth of burial, soil type, and time of year; as well as plant characteristics such as plant size, depth of origin of the root fragment, and plant age, reproductive status, biotype and vigor [67].

In general the capacity of rush skeletonweed to regenerate from root fragments increases with the size of the fragment [23]. Rush skeletonweed root segments as small as 1 inch (2.5 cm) produced 3 buds (Kefford 1964, as cited by [60]). In a laboratory experiment, Cuthbertson [23] observed little to no shoot production from 0.4 inch (1 cm) rush skeletonweed root cuttings at all burial depths and soil types, while shoots from fragments 0.8 to 1.5 inches (2-4 cm) long emerged from up to 16 inches (40 cm) deep in sand. Fragments this small would likely die of desiccation in the field.

In general, the capacity of rush skeletonweed to regenerate from root fragments decreases as the depth of burial increases, but this also varies with soil type. Shoot growth and emergence from taproot cuttings are generally greater in sandy soils than in clays. Fragments 1.5 inches (4 cm) long were unable to emerge from 4 inches (10 cm) deep in heavy clay soil, and were able to emerge from all burial depths up to 16 inches (40 cm) deep in sand [23].

Root fragments had different sprouting capacities at different times of year in eastern Washington. Root sections formed buds from October to March, while bud formation was nearly zero during June, and increased in August and thereafter, decreasing in November. Decline in shoot production coincides with increased day length and flower stem initiation [80].

Rush skeletonweed plants attain the capacity to reproduce vegetatively at a very early age. Under laboratory conditions, shoots were produced by about 40% of cuttings taken from taproots of 2- to 4-week-old seedlings, and by 95% to 100% of cuttings from 5- to 7-week-old plants [23]. Excised roots averaging 7 inches (18 cm) long, from 36-day-old seedlings, produced an average of 5.8 buds per root after 21 days at 77 °F (25 °C) in darkness. Under the same conditions, 17-day-old rootlets averaging 6 inches (16 cm) in length failed to produce stem buds (Kefford 1964, as cited by [60]).

All parts of the taproot appear to be capable of producing new shoot initials, although the number of shoots produced per fragment decreased as depth of origin increased [23, 80]. Distance from the root apex had no effect on the regeneration of 1.5-inch (4 cm) sections excised from 50 day old roots. All sections regenerated and produced approximately 3 buds per section (Kefford 1964, as cited by [60]).

In Australia, different types of rush skeletonweed differ in their regenerative capacity. Root cuttings from type C plants produced greater numbers of shoot buds than those of types A and B, regardless of the root diameter, plant age or depth of origin of the cutting. Bud production increased with age in types A and C, but decreased in Type B plants (Hull and Groves 1973, as cited by [67]). Similarly, Rosenthal and others [80] observed differences in root production between the early- and late-flowering biotypes in Washington. After 6 months growth in buried cans, the early-flowering type averaged 6.7 major roots per plant and the late-flowering type averaged 10.7 major roots per plant. After 18 months, the early-flowering plant showed no further increase in
root numbers, while the late-flowering plants averaged 16 major roots per plant [80].

Regeneration from root fragments may also depend on the reproductive status of the plant from which the fragment originates. Regeneration occurred on 7% of cuttings from the top 16 inches (40 cm) of taproot from reproductive plants, compared with 15% for vegetative plants [23].

SITE CHARACTERISTICS:

It seems that a particular combination of climate, soil type and disturbance is most favorable to dense infestations of rush skeletonweed. According to Wapshere and others [99], dense stands of rush skeletonweed are rare in western Europe because areas of optimal climate are limited and widely scattered, only small areas of suitable sandy soil are available, and the type of cultivation (wheat/fallow) most associated with dense stands of rush skeletonweed is rarely practiced in the western Mediterranean. The possibility of such a combination of circumstances co-occurring together for a sufficiently long time for population build-up to occur to dense levels in the western Mediterranean is slight.

General climate:

Rush skeletonweed occurs over a wide range of climatic conditions. The greater part of its native range lies in Mediterranean and steppe climates. Rush skeletonweed does not occur in the cool, maritime climates of extreme western Europe nor in arid, desert climates of central Algeria, southern Iraq or central Australia. Humid, subtropical climates are apparently suitable for rush skeletonweed, provided the winters are cool. Optimum conditions for rush skeletonweed in Australia include cool winters, warm summers without severe summer drought, a distinct increase in precipitation at the onset of the cool season, and additional spring rainfall [58,60,67]. Bioclimatic prediction techniques indicate virtually all of the western Australian wheatbelt is climatically suitable for rush skeletonweed ([67] and references therein). Summer-dry montane and Mediterranean habitats are favored by rush skeletonweed in the western U.S. [40].

Induction of bolting and flowering in rush skeletonweed is somewhat dependent on the extent of cold temperature exposure (vernalization) [15,21]. Rush skeletonweed has no absolute requirement for vernalization although this process accelerates both bolting and flowering [8,15,21,67]. The distribution limits in southeastern Australia almost coincide with the isotherm for a mean minimum temperature of 41 °F (5 °C) over the months of April to July or with that for a mean monthly temperature of 50 °F (10 °C) from June to August. The southern limit of rush skeletonweed in the eastern Mediterranean also correlates rather well with the incidence of low winter temperatures. There have been no records of frost damage in rush skeletonweed from any part of its range, and even newly established seedlings appear to be frost resistant [58].

A comparison of altitudinal limits in both hemispheres and the latitudinal limit of rush skeletonweed in northern Europe indicates that summer temperatures of at least 59 °F (15 °C) are required for flowering and seed formation [58]. Rush skeletonweed requires a photoperiod of 12 to 14 hours to induce bolting and flowering [15].

Panetta and Mitchell [68] present the following averages for rush skeletonweed's Australian temperature profile:

<table>
<thead>
<tr>
<th>Mean Annual Air Temperature (°C)</th>
<th>Min (°C)</th>
<th>Max (°C)</th>
<th>Range (°C)</th>
<th>Mean temperature of wettest quarter (°C)</th>
<th>Mean temperature of driest quarter (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16.3</td>
<td>4.0</td>
<td>30.7</td>
<td>26.7</td>
<td>13.9</td>
<td>19.3</td>
</tr>
</tbody>
</table>

Temperature requirements are less likely to limit rush skeletonweed distribution than are summer storms that result in premature germination of rush skeletonweed seeds [21,58].

Soil characteristics, soil moisture:
Where rush skeletonweed is native, it appears to favor coarse-textured, well-drained soils such as sand dunes, granite outcrops, and other coarse soils (Iljin 1930, as cited by [58]). In all parts of its native range the soils on which rush skeletonweed grows appear to be calcareous or only mildly acid [58,60].

In general, the soils on which dense infestations of rush skeletonweed were found in Mediterranean Europe had a relatively high percentage of sand and were low in nutrients [91,92]. Rush skeletonweed occurred where soils had 72.6 to 81.5% sand, 0.75 to 1.61% organic N, and 0.43 to 0.24% assimilable phosphate (P$_2$O$_5$). Sites with dense populations of rush skeletonweed had 2 main soil types: little disturbed, degraded dunes with 92.6% sand, 41.2% Ca, 0.64‰ organic N, 0.11‰ assimilable P$_2$O$_5$; and disturbed sites (cultivated sites or roadsides) with 81.2% sand, 6.1% Ca, 1.29‰ organic N, and 0.32‰ assimilable P$_2$O$_5$ [99]. According to Wapshere and others [99], the optimal nutrient level for rush skeletonweed is relatively low, and competition (promoted by high nutrient levels) is of much greater relative importance to rush skeletonweed survival than nutrient availability.

In Australia, rush skeletonweed occurs on all but heavy clay soils and develops best and is most abundant on deep sands, sandy loams, and sandy-clay loams [19,60,67]. Rush skeletonweed plants generally do not establish on undisturbed, fine-textured soils [58,67]. In a review article, Panetta and Dodd [67] provide evidence of rush skeletonweed occurrence on sandy soils with pH values in the range of 5.3 to 8.9, and its absence on adjacent, heavier textured soils. Similarly, Moore [60] indicates rush skeletonweed occurrence on soils with pH ranges from 4.5 to 8.0 in Australia.

In Washington state, rush skeletonweed occurs most commonly on sites characterized by one of 2 distinct soil types. One is extremely shallow soil over bedrock, the majority of which occurs in the channeled scablands and is typified by the presence of wavyleaf thistle. The other consists of sandy to gravelly soils primarily of glacial origin, and often indicated by the presence of Dalmatian toadflax (see Habitat Types And Plant Communities). These 2 soil types correspond well to soils favored by rush skeletonweed in its native range where rush skeletonweed occurs primarily on either sandy steppes or stony habitats (Ilgin 1930 as cited by [58,62]). Observations in southwestern Idaho also indicate that rush skeletonweed is most common on coarse-textured, deep, well-drained soils. Fine-textured soils appear to impede rush skeletonweed root development and regeneration by buds on lateral roots [54].

Soil types that favor establishment and persistence of rush skeletonweed support mesic-xeric to xeric plant communities. These communities naturally display very low density plant cover which provides rush skeletonweed seedlings a favorable environment for establishment. The coarse textured soils also allows for lateral root growth and horizontal spread of rush skeletonweed [62,63]. Rush skeletonweed also occasionally occurs in deeper and/or finer textured soils when spread by root fragments [63]. Because of the high degree of conformity of rush skeletonweed infestation to shallow or sandy-gravelly soil types, Old [63] predicts that the rush skeletonweed infestation in extreme eastern Washington will remain primarily one of rangeland. Sites with an artificial gravel substrate (e.g. road fill, railroad fill, gravel pits) are also known to be susceptible to rush skeletonweed establishment [63].

Precipitation:

In the western Mediterranean, maximum densities of rush skeletonweed occur in areas with a relatively hot, dry summer without a heavy drought, with an average rainfall of 16 to 28 inches (400-700 mm), relatively evenly distributed throughout the year. In this region, a wetter climate may inhibit rush skeletonweed by promoting competition [99]. Sites in Greece where rush skeletonweed was observed had average annual rainfall ranging from 15 to 25 inches (384-642 mm) [98]. In Australia rush skeletonweed has been recorded from districts with mean annual rainfalls ranging from 9 to 60 inches (230-1520 mm) [58,60,100].

According to a review by Liao [54], rush skeletonweed occurs in areas ranging from sites in eastern Washington where the average annual precipitation is less than 10 inches (250 mm), to sites in western Oregon where the average annual precipitation exceeds 40 inches (1000 mm).
Timing of precipitation is important for establishment and spread of rush skeletonweed. In areas where summer showers followed by severe drying are common, the rush skeletonweed seed bank is likely to be depleted since seedlings are likely to die of desiccation, thus limiting its spread by seed [21, 58, 64, 82].

**Elevation/ aspect**
The elevational range of rush skeletonweed is from close to sea level in Australia and Europe up to 5,100 feet (1,550 m) in Central Europe, Cyprus and the Southern Highlands of New South Wales, and up to 5,900 feet (1,800 m) in Armenia. Between the Caspian Sea and Mongolia rush skeletonweed is found only on areas of elevated land and not in the surrounding low-lying steppe (Iljin 1930, as cited by [58]).

In Australia, infestations along roadsides and sheep tracks are common at 4,000 to 4,900 feet (1,200-1,500 m), but these plants do not flower until the end of March, by which time the flowering season below an altitude of 2,000 feet (600 m) has been completed. It has been observed that plants growing near 5,400 feet (1,650 m) in Australia may not flower until just before the onset of winter, so that little or no seed is set [58].

Rush skeletonweed occurs from sea level to 2,000 feet (600 m) in California [45], and up to 3,000 feet (950 m) in British Columbia [40].

No rush skeletonweed populations were found on north facing slopes in eastern Washington [62].

**Latitude/longitude:** In its native range, rush skeletonweed is found between 35° and 55° N latitude, and Australian infestations occur between 26° to 38 ° S latitude. In North America, rush skeletonweed is most common in the wheat-growing plains of the Palouse between 38° and 48° N latitude [58].

Induction of bolting and flowering in rush skeletonweed is somewhat dependent on day length [15, 21], requiring between 8 and 14.5 hours of daylight [8]. Delays in flowering may be anticipated in low latitudes, but are unlikely to affect the distribution of rush skeletonweed in northern Australia, where day length varies from 12 to 13 hours [21, 58]. Rush skeletonweed requires a photoperiod of 12 hours at low temperatures (50 to 59 °F (10-15 °C)) and 14 hours at higher temperatures (72 to 81 °F (22-27 °C)) to induce bolting and flowering [15].

**Evidence of disturbance:**
Rush skeletonweed is able to thrive where soil disturbance occurs. Removal of natural vegetation and/or cultivation may provide opportunities for rush skeletonweed to establish. These disturbances create a favorable seedbed for rush skeletonweed germination and seedling establishment and remove competition [54, 100].

Throughout Europe and the Mediterranean islands, rush skeletonweed is primarily a species of disturbed road sides although it is also found on river banks, dry river beds, degraded coastal dunes, and eroded ground. It may be extremely abundant on "waste land" and in fallow and abandoned fields but is seldom reported as a troublesome weed in crops [58, 99]. Soil disturbance is extremely favorable to rush skeletonweed seedling establishment. Disturbance by cultivation, soil erosion, and road grading and the weakening of the original vegetation cover by overgrazing and/or drought, have provided rush skeletonweed with ample opportunity to colonize and spread in Europe, Asia, North America, and Australia [58].

Frequency of disturbance may be important to rush skeletonweed densities. In Greece, rush skeletonweed was rare (<1 plant/100m²) in continuously cultivated situations, more common in cereal cultivation (2-7 plants/m²), and most abundant on recently abandoned fields (30-60 plants/m²). Population densities were lower in long abandoned and rough pasture situations (2-20 plants/m²) [98].

In Australia, rush skeletonweed occurs at highest densities on cultivated land under a wheat/fallow system,
and in volunteer annual pastures that follow crops [58,60,67]. The inland distribution of rush skeletonweed in Australia often coincides with the limit of wheat cropping [58]. It forms tall, dense, almost continuous thickets on roadsides and other places subject to repeated disturbance, such as pastures [58,60,67]. Rush skeletonweed does not usually invade native or improved pasture [68], but may establish dense stands in native pasture weakened by drought and overgrazing [58].

In North America, rush skeletonweed is found along railroads, roadsides [18,34,89,96], fields [18,34,89,103], "waste places" [18,103], and disturbed ground [45]. Areas of road and rail fill and other areas of artificial gravel substrate are particularly susceptible to infestation by rush skeletonweed. In Oregon the use of gravel from an 80 acre (32 ha) gravel pit which was heavily infested with rush skeletonweed was the major means of distribution of rush skeletonweed for that state [62].

According to Harris [40], in Canada, rough fescue range in good condition is resistant to rush skeletonweed invasion. Rush skeletonweed may occur in elk yards and around salt licks, but not in adjacent areas with vigorous native vegetation. Rush skeletonweed rosette leaves are palatable to cattle and wildlife, so small amounts in rangeland are not considered problematic. The more serious problem occurs on overgrazed sites, and those disturbed by off-road vehicles or other means. On these sites, rush skeletonweed is likely to become the dominant herbaceous species. Rush skeletonweed invades disturbed open-canopied forest and logged areas [40].

SUCCESSIONAL STATUS:
Rush skeletonweed appears to be an early seral species that establishes well on disturbed soil. It is not known how long a rush skeletonweed population will persist on a site in the absence of disturbance. There are no studies of rush skeletonweed competition with native species in areas where it is invasive. Competition studies with subterranean clover in Australia indicate that rush skeletonweed is somewhat tolerant of shade [58], and a study in Washington state indicates that rush skeletonweed can occur under a ponderosa pine canopy, although the disturbance history of that site is not described [62]. On some sites, a decline in density of rush skeletonweed may lead to dominance by other nonnative invasive species [61].

Reduction in numbers of established rosettes of rush skeletonweed as a result of competition from subterranean clover has been demonstrated (Moore and Robertson 1964, as cited by [58]). A reduction in illumination to 10% to 20% of full daylight did not prevent rush skeletonweed seedling establishment, but plants did not flower and had slight to marked etiolation. A reduction to 50% of full daylight reduced but did not prevent some flowering and seed setting in rush skeletonweed. A reduction in light to below 1% of full daylight at soil level completely prevented seedling establishment [58]. These results suggest that cover crops producing shade of this order for several months during the winter rosette stage of first-year plants may reduce infestations of rush skeletonweed. The major part of competition appears to be for light, but root competition for water and nutrients may also arise [58].

Due to limited shade tolerance of both rush skeletonweed seedlings and mature plants, it is seldom found under trees. This is consistent for data from north and central Idaho, Oregon and most of Washington. However, rush skeletonweed plants were found beneath ponderosa pine trees at a site in Stevens county, Washington, and seemed to prefer that location at that site. The author suggests that genetic modification of characteristics such as shade tolerance could in the long run cause shifts in ecologic amplitude of rush skeletonweed [62].

A decline in rush skeletonweed, presumably due to the establishment and spread of biological control agents, was observed in Spokane County, Washington. The vacant lots once "noticeably infested" with rush skeletonweed became dominated, instead, by spotted and/or diffuse knapweed over a period of 5 to 10 years [61].

SEASONAL DEVELOPMENT:
Seasonal development in rush skeletonweed populations may vary with geographic location, elevation, precipitation, and plant biotype.

In Europe, rush skeletonweed is described as biennial. However, in Australia and North America it is described as perennial, although some confusion has arisen due to its unusual habit of flowering in its 1st year [62].

The life cycle of rush skeletonweed in Australia is described by several authors (e.g. [19,37,58,60]). The annual growth cycle of established plants begins with rosette formation in early autumn, usually in April or May. One to several new rosettes form on the root of the parent plant and grow throughout winter and spring. Peak seedling emergence is in June, although seedlings may establish as early as April [65]. There is no evidence for a spring seedling crop from seeds overwintered in the soil, although if viable seeds are present in spring they may germinate if moisture is sufficient. Spring germinated plants did not flower in the same summer in the field or in the greenhouse at Canberra [58].

Seedlings remain in the cotyledon stage for several weeks during which time the radicle elongates rapidly to initiate a deep taproot system. Seedling rosette growth proceeds slowly during winter months, whereas the taproot grows rapidly, about 0.4 inch (1 cm) per day. The ratio of root to top growth depends on air and soil temperatures [58]. Rush skeletonweed plants usually produce a flowering stem the 1st year of growth, although crowded plants on poor soil may fail to flower the 1st season. In this case, the flowering stem may persist for the greater part of winter [58], although this is uncommon [67].

Aerial flowering stems are initiated in spring from the central growing points of rush skeletonweed rosettes and begin to elongate in spring (September and October in Australia) [60,67]. While the flowering stem elongates and branches, the rosette leaves usually die, leaving the plant virtually leafless over summer [67]. Under greenhouse conditions, the period of inflorescence development (i.e. time taken from the start of stem elongation to the opening of the first flower) ranged from about 84 to 104 days, depending on the geographic origin of seed material (Hull and Groves 1973, as cited by [67]).

In western Australia, rush skeletonweed flowering generally begins in mid- to late December (slightly earlier at lower latitudes and at lower elevations), and ceases around April. Flowering and seed production reach a peak in mid-summer (January and February) and continue at low rates in some plants until late May [28]. Rush skeletonweed flowers open early one morning, close again before sunset and do not open again the following day. In hot, dry weather, flowers may remain open for only a few hours [58]. Within 4 days the achene is fully grown and the pappus extruded beyond the tip of the involucre [24]. As rush skeletonweed seeds mature any remaining basal rosette leaves senesce, but flower stalks remain green until autumn [60].

Between 10 and 20 days after flowering, rush skeletonweed plants begin to shed seed, and seeds are carried away by the wind [58]. Under greenhouse conditions, developed seeds were shed 13 to 15 days after flowering, and rates of seed maturation increased under higher temperatures. Small numbers of germinable seeds were obtained as early as 3 days following flowering ([67] and references therein). The period of rush skeletonweed seed production varies from a few weeks to 24 weeks [28], but usually occurs over a relatively long period. Germination may take place immediately if the seed arrives at a spot where soil moisture is adequate, but the main germination period begins with the onset of the 1st effective autumn rains [58].

The flowering stem begins senescence during early autumn and eventually dies completely, breaking off easily when dead. New rosettes appear at ground level during stem senescence, thereby restarting the annual growth cycle. Seedlings may appear at any time from summer to winter, but are most common in autumn and early winter [19]. New rosettes are formed in response to cultivation at any time of the year [60]. The timing of death and regeneration of above-ground parts varies in any population of rush skeletonweed, causing some overlap of stages at the beginning and end of the growing season [19].

Accounts of seasonal development of rush skeletonweed in the northern hemisphere are limited, but it appears
to follow the same pattern as that observed in Australia. Liao [54] observed the phenology of rush skeletonweed at 2 sites in Idaho over 2 years. Most rush skeletonweed seeds germinate with fall precipitation, overwinter as rosettes, and bolt in spring. Flowering and seed production begin in mid-summer and continue as late as October. Rush skeletonweed leaves wither and die during flowering. The following table presents recorded phenological events in Idaho [54]:

<table>
<thead>
<tr>
<th>Phenological event</th>
<th>Shrub Garden site</th>
<th>Orchard site</th>
</tr>
</thead>
<tbody>
<tr>
<td>bolting</td>
<td>prior to 5/20</td>
<td>4/26</td>
</tr>
<tr>
<td>branching</td>
<td>prior to 5/20</td>
<td>5/18</td>
</tr>
<tr>
<td>1st buds</td>
<td>6/23</td>
<td>7/5</td>
</tr>
<tr>
<td>1st flowers</td>
<td>7/8</td>
<td>7/13</td>
</tr>
<tr>
<td>1st seeds</td>
<td>7/21</td>
<td>7/26</td>
</tr>
</tbody>
</table>

Bud formation, anthesis, and seed set at one site occurred earlier that at the other site by about 1 week, probably due to elevational lag response (256 feet (78 m) elevation difference). Plants began budding, flowering, and setting seed earlier in the dry year (1994). Precipitation at these 2 sites was 8 to 10 inches (200-250 mm) in 1994, and 13 to 17 inches (320-420 mm) in 1995 (Orchard and Shrub Garden, respectively). Even in the drier year, rush skeletonweed produced seed throughout the summer. Rush skeletonweed flowers at a time in this region that is between the flowering times of native plants, most of which flower in late spring or early summer [54].

Flowering times at other locations in the U.S. are reported as follows:

<table>
<thead>
<tr>
<th>Place</th>
<th>Flowering dates</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intermountain and Pacific Northwest</td>
<td>July-Sept</td>
<td>[18,46]</td>
</tr>
<tr>
<td>Blue Ridge</td>
<td>June thru August</td>
<td>[103]</td>
</tr>
<tr>
<td>West Virginia</td>
<td>July, August</td>
<td>[89]</td>
</tr>
<tr>
<td>Northeastern U.S.</td>
<td>July-September</td>
<td>[34]</td>
</tr>
</tbody>
</table>

In Canada, rush skeletonweed rosettes die-back in winter and regrow in April, initially without latex. Bolting starts in early May, with each rosette producing a single upright stem. Preflowering stems have numerous green branches and inconspicuous linear leaves, but the rosette and stem leaves die as flowering starts. A succession of flowers is formed from early August until the stems die in the fall. In Canada, October frost may curtail flowering and induce rosette formation [40].

A phenological account of rush skeletonweed on a site in southern British Columbia is given by Martin [56].

<table>
<thead>
<tr>
<th>Date</th>
<th>Phenological event</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 April</td>
<td>new growth beginning to form on side of old rush skeletonweed stems at a point just below soil level; no overwintering rosettes found; less than half the previous year's plants were showing new shoot initiation; no latex</td>
</tr>
</tbody>
</table>
Species: Chondrilla juncea

FIRE ECOLOGY

SPECIES: Chondrilla juncea

- FIRE ECOLOGY OR ADAPTATIONS
- POSTFIRE REGENERATION STRATEGY

FIRE ECOLOGY OR ADAPTATIONS:

Fire adaptations:
Information regarding fire adaptations of rush skeletonweed is not available in the literature. Established rush skeletonweed plants have deep, extensive perennial root systems and are known to sprout following injury (e.g. cutting, grazing, herbicide or insect damage) to rosettes or taproots (see Asexual regeneration). Sprouting can occur almost anywhere on the remaining root system [37,58,67,73], reputedly from buds as deep as 3 feet (1 m) [58,67]. This adaptation would allow rush skeletonweed to survive even severe fire, depending on site conditions.

Rush skeletonweed is also capable of establishing from seed. Rush skeletonweed seeds are considered short-lived under field conditions and generally survive for less than 6 to 18 months [64,82]. The tolerance of rush skeletonweed seeds to heating is unknown. Rush skeletonweed seeds can also be dispersed by wind over long distances [67], although it is not known whether rush skeletonweed is more or less likely to establish from seed after fire. According to anecdotal evidence presented by Asher and others [5], rush skeletonweed established and spread after 2 successive wildfires in Idaho (see Postfire colonization potential for more details).

Fire regimes:
Rush skeletonweed occurs primarily in agricultural and rangeland communities in the western U.S. and southwestern Canada, where historic fire regimes have been dramatically altered due to massive disturbances associated with human settlement (e.g. [62]). Rush skeletonweed is associated with cheatgrass in some areas. Cheatgrass expansion has dramatically changed fire regimes and plant communities over vast areas of western rangelands by creating an environment where fires are easily ignited, spread rapidly, cover large areas, and occur frequently [105]. Short fire return intervals in cheatgrass-dominated communities (<10 years [70,101]) may favor rush skeletonweed, with its large root reserves and the ability to sprout after injury. More research and field observations are needed to understand how rush skeletonweed responds to the current fire ecology of these areas.

The historic fire regimes of native communities in which rush skeletonweed sometimes occurs are of varied
frequency and severity. Rush skeletonweed did not occur in these communities at the time in which historic fire regimes were functioning, but has established since fire exclusion began. It is unclear how historic fire regimes might affect rush skeletonweed populations. It is also unclear how the presence of rush skeletonweed might affect these fire regimes. In general, in ecosystems where rush skeletonweed replaces plants similar to itself (in terms of fuel characteristics), it may alter fire intensity or slightly modify an existing fire regime. However, if rush skeletonweed is qualitatively unique to the invaded ecosystem, it has the potential to completely alter the fire regime [25]. No examples of fire regimes altered by rush skeletonweed invasion are described in the available literature.

The following table provides fire return intervals for plant communities and ecosystems in which rush skeletonweed may be found. If you are interested in the fire regime of a plant community that is not listed here, please consult the complete FEIS fire regime table.

<table>
<thead>
<tr>
<th>Community or Ecosystem</th>
<th>Dominant Species</th>
<th>Fire Return Interval Range (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>silver sagebrush steppe</td>
<td>Artemisia cana</td>
<td>5-45 [44,76,104]</td>
</tr>
<tr>
<td>sagebrush steppe</td>
<td>A. tridentata/Pseudoroegneria spicata</td>
<td>20-70 [69]</td>
</tr>
<tr>
<td>basin big sagebrush</td>
<td>A. tridentata var. tridentata</td>
<td>12-43 [81]</td>
</tr>
<tr>
<td>mountain big sagebrush</td>
<td>A. tridentata var. vaseyana</td>
<td>15-40 [3,13,59]</td>
</tr>
<tr>
<td>Wyoming big sagebrush</td>
<td>A. tridentata var. wyomingensis</td>
<td>10-70 (40**) [95,106]</td>
</tr>
<tr>
<td>cheatgrass</td>
<td>Bromus tectorum</td>
<td>&lt; 10 [70,101]</td>
</tr>
<tr>
<td>California steppe</td>
<td>Festuca-Danthonia spp.</td>
<td>&lt; 35 [69,88]</td>
</tr>
<tr>
<td>juniper-oak savanna</td>
<td>Juniperus ashei-Quercus virginiana</td>
<td>&lt; 35</td>
</tr>
<tr>
<td>western juniper</td>
<td>J. occidentalis</td>
<td>20-70</td>
</tr>
<tr>
<td>Rocky Mountain juniper</td>
<td>J. scopulorum</td>
<td>&lt; 35 [69]</td>
</tr>
<tr>
<td>wheatgrass plains grasslands</td>
<td>Pascopyrum smithii</td>
<td>&lt; 5-47+ [69,76,104]</td>
</tr>
<tr>
<td>interior ponderosa pine*</td>
<td>Pinus ponderosa var. scopulorum</td>
<td>2-30 [2,7,50]</td>
</tr>
<tr>
<td>red-white-jack pine*</td>
<td>P. resinosa-P. strobos-P. banksiana</td>
<td>10-300 [29,43]</td>
</tr>
<tr>
<td>mountain grasslands</td>
<td>Pseudoroegneria spicata</td>
<td>3-40 (10**) [1,2]</td>
</tr>
<tr>
<td>Rocky Mountain Douglas-fir*</td>
<td>Pseudotsuga menziesii var. glauca</td>
<td>25-100 [2,3,4]</td>
</tr>
<tr>
<td>California oakwoods</td>
<td>Quercus spp.</td>
<td>&lt; 35 [2]</td>
</tr>
<tr>
<td>oak-hickory</td>
<td>Quercus-Carya spp.</td>
<td>&lt; 35 [97]</td>
</tr>
<tr>
<td>blue oak-foothills pine</td>
<td>Q. douglasii-P. sabiniana</td>
<td>&lt; 35</td>
</tr>
<tr>
<td>Oregon white oak</td>
<td>Q. garryana</td>
<td>&lt; 35</td>
</tr>
<tr>
<td>western redcedar-western hemlock</td>
<td>Thuja plicata-Tsuga heterophylla</td>
<td>&gt; 200 [2]</td>
</tr>
</tbody>
</table>

*fire return interval varies widely; trends in variation are noted in the species summary
**mean

**POSTFIRE REGENERATION STRATEGY [87]:**
Caudex/herbaceous root crown, growing points in soil
Geophyte, growing points deep in soil
Ground residual colonizer (on-site, initial community)
Initial off-site colonizer (off-site, initial community)
Secondary colonizer (on-site or off-site seed sources)

FIRE EFFECTS

SPECIES: Chondrilla juncea

- IMMEDIATE FIRE EFFECT ON PLANT
- DISCUSSION AND QUALIFICATION OF FIRE EFFECT
- PLANT RESPONSE TO FIRE
- DISCUSSION AND QUALIFICATION OF PLANT RESPONSE
- FIRE MANAGEMENT CONSIDERATIONS

IMMEDIATE FIRE EFFECT ON PLANT:
No information is available in the literature regarding the direct effects of fire on rush skeletonweed. Fire is likely to kill aboveground portions of rush skeletonweed plants, but unlikely to kill the deep, extensive roots of established rush skeletonweed plants.

No information is available regarding heat tolerance of rush skeletonweed seeds.

DISCUSSION AND QUALIFICATION OF FIRE EFFECT:
No additional information is available on this topic.

PLANT RESPONSE TO FIRE:
Established rush skeletonweed plants are likely to survive even severe fire because they have deep, extensive perennial root systems that are known to sprout following injury to rosettes or taproots (see Asexual regeneration). Sprouting can occur almost anywhere on the surviving root system [37,58,67,73], reputedly from buds as deep as 3 feet (1 m) [58,67].

Rush skeletonweed produces abundant, wind-dispersed seeds under favorable site conditions [67] and may, therefore, establish from seed from offsite sources following fire. It is not known whether rush skeletonweed is more or less likely to establish from seed in a postfire environment.

DISCUSSION AND QUALIFICATION OF PLANT RESPONSE:
No additional information is available on this topic.

FIRE MANAGEMENT CONSIDERATIONS:
Fire as a control agent:
No information is available regarding the use of fire as a control agent for rush skeletonweed. Rush skeletonweed is very difficult to kill due to its extensive root system. It is, therefore, unlikely that rush skeletonweed populations can be controlled by prescribed fire. Young plants may be susceptible to heat kill from hand-held burners, as has been observed with other invasive species with similar root systems (e.g. [79]).

Although it is unlikely that rush skeletonweed can be controlled with fire, using prescribed fire in fire-adapted ecosystems may discourage rush skeletonweed by encouraging the growth and vigor of native species. Caution is advised in this regard. Season of burning and other management activities (e.g. herbicide treatments, livestock and wildlife use) are important factors to consider when prescribing fire treatments for natural area restoration where nonnative invasive plants are present [52]. Additionally, land managers should always be cautious when using fire to control invasives because it may promote the establishment of other fire-tolerant invasive species [10]. More research is needed in fire adapted areas with rush skeletonweed populations.
**Postfire colonization potential:**
No experimental evidence is available regarding rush skeletonweed’s potential to establish after fire. Rush skeletonweed produces abundant, wind-dispersed seeds under favorable site conditions [67], and may, therefore establish from seed from offsite sources following fire. It is not known whether rush skeletonweed is more or less likely to establish from seed in a postfire environment.

According to anecdotal evidence presented by Asher and others [5], a 200,000 acre (81,000 ha) wildfire burned over a BLM wilderness study area in Idaho in 1992. Rush skeletonweed was not known to occur at this site until a few rush skeletonweed plants were found and controlled in 1995. In 1996 another wildfire burned the entire area again. A 1997 survey found "serious rush skeletonweed infestations widely scattered within a 60,000 acre (24,000 ha) area of the burn [5].

**Preventing postfire establishment and spread:**
The USDA Forest Service's "Guide to Noxious Weed Prevention Practices" [93] provides several fire management considerations for weed prevention in general that apply to rush skeletonweed.

When planning a prescribed burn, managers should preinventory the project area to evaluate the extent, cover, and phenology of any rush skeletonweed or other invasive plants present on or adjacent to the site, and avoid ignition and burning in areas at high risk for rush skeletonweed establishment or spread due to fire effects. Managers should also avoid creating soil conditions that promote rush skeletonweed germination and establishment. Areas of soil disturbance (e.g. those brought about by fire suppression activities) are especially susceptible to invasive plant establishment. Invasive plant status and risks must be discussed in burn rehabilitation plans. Also, wildfire managers might consider including weed prevention education and providing weed identification aids during fire training; avoiding known weed infestations when locating fire lines, monitoring camps, staging areas, helibases, etc., to be sure they are kept weed free; taking care that equipment is weed free; incorporating weed prevention into fire rehabilitation plans; and acquiring restoration funding. Additional guidelines and specific recommendations and requirements are available [36,93].

Preventing invasive plants from establishing in weed-free burned areas is the most effective and least costly management method. This can be accomplished through early detection and eradication, careful monitoring, and by limiting invasive plant seed dispersal into burned areas by [6,36,93]:

- re-establishing desirable vegetation on bare ground as soon as possible
- using only certified weed-free seed mixes when revegetation is necessary
- cleaning equipment and vehicles prior to entering burned areas
- regulating or preventing human and livestock entry into burned areas until desirable site vegetation has recovered sufficiently to resist invasion by undesirable vegetation
- detecting weeds early and eradicating them before vegetative spread and/or seed dispersal
- eradicating small patches and containing or controlling large infestations within or adjacent to the burned area

In general, early detection is critical for preventing establishment of large populations of invasive plants. Monitoring in spring, summer, and fall is imperative. Managers should eradicate established rush skeletonweed plants and small patches adjacent to burned areas to prevent or limit seed dispersal into the site [6,36,93].

The need for revegetation after fire can be assessed on the basis of the degree of desirable vegetation displaced by invasive plants prior to burning, and on postfire survival of desirable vegetation. Revegetation necessity
can also be related to invasive plant survival as viable seeds, root crowns, or rhizomes capable of reproduction. In general, postfire revegetation should be considered when desirable vegetation cover is less than about 30% [36].

Goodwin and others [35,36] provide guidelines for determining burn severity, revegetation necessity, and establishing and managing competitive plants. The following paragraphs provide some general guidelines for invasive species management after fire. See Integrated Noxious Weed Management after Wildfires for a more detailed source of this information. More research is needed specific to fire tolerance and response of rush skeletonweed to fire in specific sites and ecosystems in which it occurs.

When prefire cover of rush skeletonweed is absent to low, and prefire cover of desirable vegetation is high, revegetation may not be necessary after low- and medium-severity burns. After a high-severity burn on a site in this condition, revegetation may be necessary (depending on postfire survival of desirable species), and intensive monitoring for invasive plant establishment is critical to detect and eradicate newly established invasives before they spread [36].

When prefire cover of rush skeletonweed is moderate (20-79%) to high (80-100%), revegetation may be necessary after fire of any severity, especially if cover of desired vegetation is less than about 30%. Intensive weed management is also recommended, especially after fires of moderate to high severity [36].

Fall dormant broadcast seeding into ash will cover and retain seeds. If there is insufficient ash, seedbed preparation may be necessary. A seed mix should contain quick-establishing grasses and forbs (exclude forbs if broadleaf herbicides are anticipated) that can effectively occupy available niches. Managers can enhance the success of revegetation (natural or artificial) by excluding livestock until vegetation is well established (at least 2 growing seasons) [36].

**MANAGEMENT CONSIDERATIONS**

**SPECIES: Chondrilla juncea**

- **IMPORTANCE TO LIVESTOCK AND WILDLIFE**
- **OTHER USES**
- **IMPACTS AND CONTROL**

**IMPORTANCE TO LIVESTOCK AND WILDLIFE:**
Evidence presented in Australian and Canadian literature indicates that rush skeletonweed is consumed during particular growth phases by domestic sheep, goats, horses, and cattle, and by some wildlife species [40,56,58,67]. Rosette leaves and stems prior to flowering are more palatable to domestic sheep and other domestic animals while domestic goats and wild herbivores will consume the older, more fibrous stems as well [40,58]. The fibrous flowering stem may cause choking and loss of condition when eaten by dairy cattle [67].

Plants may be prevented from flowering where animal browsing is constant, and this may be one of the reasons for the species' lack of importance as a weed in Mediterranean countries [58]. Similarly, Harris [40] notes that small amounts of rush skeletonweed in North American rangeland are not serious because rosette leaves are palatable to cattle and wildlife. Continuous grazing keeps plants in the rosette stage during the summer months when little other green forage is available, and flowering stems form quickly if there is any interruption to grazing [67].

A review by Panetta and Dodd [67] describes sheep management programs developed on infested properties.
in Australia to utilize fodder produced by rush skeletonweed. It is claimed that some of the best fat lambs in Australia come from areas heavily infested with rush skeletonweed [67].

**Palatability/nutritional value:**
Rush skeletonweed is palatable and nutritious in the rosette stage and during flowering until the stem becomes lignified (Cuthbertson 1967, as cited by [67]).

**Cover value:** No information is available on this topic.

**OTHER USES:**
When rainfall is favorable, rush skeletonweed can be a major source of pollen and a small surplus of golden honey can be produced from its nectar [67].

In Russia, stem-boring insects produce knots of callus and solidified latex which have been investigated as a possible source of rubber (Iljin 1930, as cited by [58]).

**IMPACTS AND CONTROL:**

**Impacts:**
Rush skeletonweed apparently has most serious impacts in areas already impacted by agriculture, roads, and livestock grazing. In Australia, rush skeletonweed primarily infests cropland [58, 60, 67], while in North America, rush skeletonweed is found primarily in California and the Pacific Northwest on "abused" rangelands and roadsides, although some encroachment of cropland has occurred and may be increasing [18, 30, 58, 63, 74, 80].

According to a review by Panetta and Dodd [67], rush skeletonweed is widely recognized as the most serious weed of the Australian wheat growing regions. The tall, wiry stems of rush skeletonweed interfere with harvesting equipment, and the plants reduce yields and cause economic losses through competition for moisture, nitrogen, and other nutrients ([67] and references therein). Rush skeletonweed was first reported in Australia in 1918, and over the next 42 years it spread at an average of 15 to 20 miles (24-32 km) per year to cover an area of almost a half million square miles (130 million ha) [58]. Rush skeletonweed was so destructive to wheat production that much of the land that had historically produced wheat was shifted to pasture. In one area alone the amount of land sown to pasture increased from 46,000 acres (19,000 ha) in 1946 to 150,000 acres (61,000 ha) in 1955 (Tindale 1956, as cited by [63]).

Reviews by Sheley and others [84] and by Liao [54] suggest that rush skeletonweed can form dense monocultures on rangeland, displace native plants, reduce forage production ("dramatically"), and "threaten the cattle industry". Observations by Quinney [75] suggest that rush skeletonweed is one of the most serious of the nonnative invasive species in the Snake River Birds of Prey National Conservation Area. It initially appeared along a road there, and within 7 years was appearing around livestock watering sites within the area. Markin [55] also states that rush skeletonweed is a particularly aggressive invader of rangelands and forestlands in southern Idaho, particularly those managed as U.S. National Forests.

Harris suggests that rush skeletonweed could potentially increase on cropland and disclimax rangeland within the ecozones in which it occurs in Canada (see Habitat Types And Plant Communities) and cause economic loss [40].

**Control:**
Rush skeletonweed is difficult to control in some situations. Prevention is the most cost-effective and least labor-intensive approach to control nonnative invasive species [85]. Small infestations can be eradicated with diligent efforts using physical and/or chemical treatments. Large, dense populations are more difficult to control and require a long-term, integrated approach that employs various management techniques to reduce frequency and density of rush skeletonweed to manageable levels [84].
Although agricultural practices are unlikely to be of practical importance for controlling invasive species in rangeland and natural areas, some mention of them is included in the following discussion as they may add to further understanding of rush skeletonweed physiology and sensitivity.

Prevention:
To prevent establishment and spread of rush skeletonweed, dispersal of seeds and root fragments must be prevented, as well as vegetative spread from infested sites, such as from road shoulders, into uninfested areas [63, 84]. Seeds are dispersed by wind, water, vehicles, and machinery. A review by Sheley and others [84] suggests avoiding driving vehicles and machinery through rush skeletonweed-infested areas during the seeding period, and washing the undercarriage of vehicles and machinery before leaving infested areas. Livestock should not graze rush skeletonweed-infested areas during seed formation. Livestock grazing infested ranges should be transported to a holding area for 10 to 14 days before moving to uninfested range [84].

Sheley and others [84] also recommend proper livestock grazing as essential to maintain competitive grass cover, which will help limit rush skeletonweed encroachment. A grazing management plan should be developed for pasture and range sites involved in rush skeletonweed prevention programs. Grazing systems should include altering season of use and stocking rates, rotating livestock to allow plants to recover before being regrazed, and promoting plant litter accumulation [84].

An integral part of any weed prevention program is to contain infestations neighboring uninfested areas, and to contain rush skeletonweed along highways, railways, and waterways [84]. In Adams County, Washington, a policy was adopted that all rush skeletonweed infestations west of a line that demarcated densely infested rangeland from the remainder of the county were to be controlled using chemical and biological controls. Buffer strips, 300 feet (90 m) in width, were established where large infestations bordered cultivated land. Complete control was maintained along rights-of-way. The purpose of the boundary line and buffer zones was to place a containment line around the worst infestations and slowly shrink those areas over the next several years [83]. No results or follow-up publications are available.

Monitoring, detecting new infestations, and implementing eradication programs are important parts of preventing spread of rush skeletonweed. Detect weed infestations early with systematic surveys along weed dispersal corridors. Once an infestation is found, an eradication plan should be designed and implemented, including an outline of the infestation boundaries, control treatments, control schedule, revegetation plans, follow-up monitoring, and costs [47, 84, 108].

Integrated management: A review by Sheley and others [84] suggests that no single treatment provides long-term control of rush skeletonweed, so an integrated strategy must be adopted. The first line of defense is to prevent introductions of rush skeletonweed with systematic surveys, early detection, and implementation of an eradication program on small infestations. Once rush skeletonweed becomes established, integrating various combinations of competitive plantings, crop-pasture rotations, domestic sheep grazing, biological control agents, and herbicides may reduce rush skeletonweed to manageable levels [84].

Examples of integrated control strategies are given within the following sections where applicable and available.

Physical/mechanical:
Physical and mechanical control methods used for rush skeletonweed control include hand-pulling or digging, cutting or mowing, and plowing or cultivation.

According to Sheley and others [84], hand-pulling can provide effective control for very small rush skeletonweed infestations. Successful hand-pulling requires removal of plant growth 2 or 3 times per year for 6 to 10 years because new plants will emerge from severed roots and possibly from buried seeds. Removing
rash skeletonweed plants is easier when the soil is wet. Pulled plants should be destroyed by burning in a very hot fire to ensure seed and root destruction [84].

Mowing rash skeletonweed infestations regularly may reduce aerial biomass, root biomass, root carbohydrate, and seed crop. McLellan [57] found that rash skeletonweed root biomass and regenerative capacity decreased with increased mowing frequency as did basal rosette production. Shoot regenerative capacity decreased with increased mowing frequency in the 1st year of study, but not in the 2nd. Mowing may reduce rash skeletonweed ability to spread vegetatively. There was a general reduction in seed production although seed viability was not affected [57].

Cutting plants close to the surface produces large multiple-stemmed plants without much increase in rosette numbers. Severing the roots at greater depth without soil mixing leads to some increase in rosette numbers through the appearance of fresh growth from lateral roots as well as from the taproot [58].

Rush skeletonweed response to cultivation depends upon frequency of cultivation, management of fields during the fallow phase, and age of rush skeletonweed plants [58,99]. Cultivation in the wheat-fallow system of cereal farming in Australia initially favored rush skeletonweed survival and spread. In this system cultivation is frequent enough to increase rush skeletonweed density due to the plant's ability to regenerate from severed root pieces (see Asexual regeneration), but not frequent enough to decrease their survival [19,60,67]. Surviving rush skeletonweed plants thrived because they had little competition in the fallow phase. Population growth rates tend to increase with the frequency of cultivation until the interval between successive cultivating is reduced to approximately 8 weeks, when plant survival is adversely affected [19]. Daughter rosettes are easier to kill since they have smaller carbohydrate reserves than those arising from taproots. Decreases in rosette densities are greatest following cultivation in dry soil, as root fragments are highly prone to desiccation [23,58,67].

Rush skeletonweed seedlings may be more easily controlled by pulling or cultivation than older plants ([62] and references therein). However, rush skeletonweed seedlings may form shoot buds from root fragments as young as 2 weeks old, and 95% to 100% of 5- to 7- week-old seedlings can regenerate from root fragments [23].

Weeding (e.g. hoeing or pulling of other plants) around established rush skeletonweed plants may result in a crop of satellite rosettes if lateral roots close to the surface become severed. Rosettes develop at the severed end of detached root [58].

Fire: See Fire Management Considerations.

Biological control
of invasive species has a long history, and there are many important considerations to be made before the implementation of a biological control program. The reader is referred to other sources [78,102] and the Weed Control Methods Handbook [91]for background information on biological control. Additionally, Cornell University, Texas A & M University, and NAPIS websites offer information on biological control.

Several organisms including insects, viral particles, and fungi, have been intensively studied as potential biological control agents for rush skeletonweed, and an abundance of literature is available on the effects of introduced agents on rush skeletonweed in Australia (e.g. [11,20,38]) and North America (e.g. [17,30,57,73,90]). The following information on biological control of rush skeletonweed is based primarily on literature reviews, as a thorough treatment of this literature is beyond the scope of this review.

The effectiveness of biological control agents on rush skeletonweed is limited primarily by the genetic variability of rush skeletonweed populations [16], and also by the level of interspecific and intraspecific competition between plants in the particular situations where they occur [99], including the effects of other
control treatments (e.g. [17,27,57,73]).

The first effective biological control program for rush skeletonweed, involving several control agents, was established in Australia in the 1960s. These agents include the gall mite (Erionyssus chondrilli), the gall midge (Cystiphora schmidti), and the rust fungus (Puccinia chondrillina); the latter being the most effective [38]. Effectiveness of the rust fungus is, however, limited by the genetic variability of rush skeletonweed populations in Australia [11]. Successful control of the most widespread type was achieved by the 1971 release of the rust; however, the reduction in populations of that genotype resulted in the spread of the rust-resistant types, previously suppressed by the competitive dominance of the rust-susceptible type [38].

Subsequently, these 3 biological control agents have been released for control of rush skeletonweed in North America, as follows [31,71,72,92].

<table>
<thead>
<tr>
<th>Agent name</th>
<th>Type of agent</th>
<th>States established</th>
<th>Feeding site/effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cystiphora schmidti</td>
<td>gall midge</td>
<td>CA, ID, OR, WA</td>
<td>Rosette, leaves, stem. Reduces photosynthesis and stresses plant</td>
</tr>
<tr>
<td>Eriophyes chondrilli</td>
<td>gall mite</td>
<td>CA, ID, OR, WA</td>
<td>Rosette, leaves, stem. May kill seedlings or young plants, reduces flower and seed production; most effective of the 3 in PNW</td>
</tr>
<tr>
<td>Puccinia chondrillina</td>
<td>rust fungus</td>
<td>CA, ID, MD, OR, VA, WA</td>
<td>Rosettes, leaves, stem. May kill young plants, stresses older plants</td>
</tr>
</tbody>
</table>

Despite reports of impacts on rush skeletonweed by biological control agents (e.g. [30,51,61,72,83,90]), Prather [73] reports that rush skeletonweed continues to dominate large areas in the Pacific Northwest.

The success of biological control agents is linked to climatic differences between their place of origin and place of introduction [31,55,56], to different rush skeletonweed biotypes [31,40], and to native parasites and predators that attack introduced biological control agents [55,71].

Martin [56] provides observations of phenological development of rush skeletonweed in southern British Columbia and notes that no overwintering rosettes were found. Rosettes are particularly important as the overwintering locus for both the gall mite and the rust [56]. Markin [55] reports that while biological control agents have given acceptable control in California, they are less effective in the Pacific Northwest. He suggests that these agents are not adapted to the climatic conditions in the Pacific Northwest. Efforts are being made to find new biological control agents from Eurasia, in the Republic of Georgia. Two agromyzid flies, some leaf-feeding caterpillars, and a small moth, Bradyrrhoa gilveolella, have shown some potential and are the subject of further study [55].

Emge and others [30] report differential reactions to infection by the rust in populations from California, Oregon, Washington and Idaho. It is evident that 3 distinct types of rush skeletonweed occur in North America, and that these types are different from those found in Australia [16,40,41], contrary to information presented by Shely and others [84]. Isozyme screening is being employed as an attempt to match rust strains from Europe with rush skeletonweed type [31].

Integrating the use of biological control agents with plant competition [37,73], herbicides [17,27], mowing [57], or other appropriate suppressive measures, may affect control of rush skeletonweed. For example, combined stresses from plant competition (from intermediate wheatgrass (Thinopyrum intermedium) and small burnet (Sanguisorba minor ssp. muricata)) and herbivory by gall mites reduced biomass of rush skeletonweed more than either stress separately. Rush skeletonweed may dominate the sparsely vegetated rangeland communities because they do not offer sufficient competition to restrict resources. These conditions may allow rush skeletonweed to overcome the growth restrictions imposed by gall mites by floral stem initiation.
from adventitious buds. If rush skeletonweed has abundant resources available, those new buds may grow more quickly than the gall mites can colonize them. Under these conditions, gall mites alone will not control rush skeletonweed [73].

Cheney [17] found that rush skeletonweed is most effectively reduced by utilizing either herbicides (picloram, dicamba, 2,4-D) or the rust organisms, exclusive of one another.

Mowing rush skeletonweed plants infested with biological control insects had no synergistic effects, but could have additive effects on rush skeletonweed spread. Both types of control reduced rush skeletonweed's ability to spread [57].

Grazing by domestic sheep can reduce or prevent seed production in rush skeletonweed. The lowest densities of rush skeletonweed were obtained under continuous, as compared with rotational, grazing. Increasing the stocking rate from 5 to 15 sheep/ha had no effect upon final weed numbers ([67] and references therein). Moderate grazing is as effective as heavy grazing in controlling rush skeletonweed because heavy grazing decreases the competitive ability of desired plant species [84]. In the northwestern U.S. some ranchers found that while heavy, dense populations of rush skeletonweed required intensive control efforts, scattered rush skeletonweed plants across well-managed pastures posed no serious decrease in livestock carrying capacity and even supplied a late season forage [61].

Chemical:
Herbicides are effective in gaining initial control of a new or severe infestation of invasive plants, but are rarely a complete or long-term solution to invasive species management [14]. Herbicides are more effective on large infestations when incorporated into long-term management plans that include replacement of weeds with desirable species, careful land use management, and prevention of new infestations. Control with herbicides is temporary, as it does not change conditions that allow infestations to occur [107]. See the Weed Control Methods Handbook for considerations on the use of herbicides in natural areas and detailed information on specific chemicals.

Once established, rush skeletonweed is extremely difficult to control using herbicides, primarily due to the difficulty of translocating herbicides into its extensive root system [58]. Degree of translocation of herbicides depends on environmental conditions, type of herbicide used, and physiological status of the plant ([67] and references therein). Since 1944, trials have been conducted on rush skeletonweed with practically every new herbicide to come on the market. In general, any chemical that eliminated rush skeletonweed also killed all other vegetation and "sterilized" soil [37,62]. Successful chemical control of rush skeletonweed usually requires an aggressive re-application program [84].

Applications of 2,4-D at the first signs of bolting inhibits inflorescence development but has no long-term effects on plant densities [60,67,82]. Repeated applications of 2,4-D may reduce rush skeletonweed densities, as would repeated mechanical removal of the rosette. Control in this manner may benefit crop production, but would need to be repeated frequently to have a long-term effect on rush skeletonweed populations [37].

Heap [42] found that rush skeletonweed can be controlled in Australia with some herbicides, and successive yearly applications are more effective than single treatments. Clopyralid alone and in mixtures with 2,4-D-amine, dicamba, or MCPA-amine, were the most effective treatments. Metsulfuron and 2,4-D-amine also were effective if applied at high rates for several years. The broadleaf type (C) appears to be less susceptible to clopyralid than other types [42].

Of several herbicides tested for rush skeletonweed control in Washington in 1964, only picloram and dicamba were "acceptably effective." These herbicides provided most consistent results when applied in fall. Due to limited rainfall in this region, picloram movement and dilution through the soil profile to a non-lethal level requires several years. Therefore production of a broadleaf crop is not likely feasible for at least 3 years after
treatment [82]. Picloram may be considered "ecologically undesirable" unless restricted to spot control [40], and is said to be incompatible with legumes [67]. Picloram remains active in the soil for up to 3 years under some conditions, and it can be highly mobile in the soil profile [91]. Picloram is often used to eradicate rush skeletonweed on road shoulders [62].

Cultural:
Seedlings of rush skeletonweed are poor competitors with most crop species. In greenhouse trials, when crop plants (e.g. oats (*Avena sativa*) and alfalfa) emerge first, rush skeletonweed does not survive [82]. Subterranean clover can be an effective competitor with established rush skeletonweed, reducing rush skeletonweed rosette density by 60% within 2 years under field conditions on the central slopes of New South Wales ([58,60] and references therein).

Dense growth of cool season annuals shades rosettes of rush skeletonweed to the extent that both densities and dry weights of rush skeletonweed are reduced considerably. A deep-rooted, perennial legume would have the added advantage of competition for soil moisture over the summer months [67].

Results presented by Prather [73] suggest that plant competition alone will not control rush skeletonweed, and that integration of plant competition with other management strategies (herbicide or biocontrol) is more tenable. Competitive effects of intermediate wheatgrass and small burnet increased with herbivory by gall mites [73].

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