SPECIES: Hypericum perforatum

Choose from the following categories of information.

INTRODUCTORY

SPECIES: Hypericum perforatum


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AUTHORSHIP AND CITATION:
Zouhar, Kris. 2004. Hypericum perforatum. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2007, September 24].

FEIS ABBREVIATION:
HYPPER

SYNONYMS:
None

NRCS PLANT CODE [182]:
HYPE

COMMON NAMES:
common St Johnswort

goatweed
Klamath weed

TAXONOMY:
The currently accepted name for common St Johnswort is *Hypericum perforatum* L. It is a member of the mangosteen or St Johnswort family (Clusiaceae) [67,69,98,99,100,199]. Some authors treat the St Johnswort family (Hypericaceae) separately (e.g. [89,90,109,127,145,152,193]). Other authors use the family name Guttiferae (e.g. [168,187]).

The Flora Europaea recognizes several varieties and hybrids of *Hypericum perforatum* in Europe [173]. Earlier treatments identify the variety *Hypericum perforatum* var. *angustifolia* in Australia [34]. It is also suggested that varying characteristics in St Johnswort simply represent a variable taxon, and no classification at the varietal level is recommended [35]. No hybrids are known to occur in Australia [34] or North America [45].

LIFE FORM:
Forb

FEDERAL LEGAL STATUS:
None

OTHER STATUS:
St Johnswort is designated a noxious weed in 7 states in the U.S. and 2 Canadian provinces [183]. It is also designated a "regulated nonnative plant species" in South Dakota. See the Plants, or APHIS, or Invaders databases for more information. St Johnswort is considered a "lesser threat" by the Kentucky Exotic Pest Plant Council. This designation applies to nonnative plant species which seem to "principally spread and remain in disturbed corridors, not readily invading natural areas" [101]. In Tennessee, St Johnswort is on "Watch List A", which includes nonnative plants for which little information is available and that may become a problem in the future [161].

DISTRIBUTION AND OCCURRENCE

SPECIES: Hypericum perforatum

GENERAL DISTRIBUTION:
St Johnswort is native to Europe, western Asia, and North Africa, and is now widely distributed through the temperate areas of the world including parts of South America, India, New Zealand, Australia, and South Africa. St Johnswort is considered a weed in much of its native range, particularly in Turkey, Italy, France, Hungary, and Sweden, mainly in poor pastures, neglected areas, and occasionally in crops [139]. Its wide distribution may in part be attributed to its cultivation as a medicinal or garden plant [45].

In Canada, St Johnswort is found mostly in the eastern provinces and British Columbia, and is absent in the prairie region [45,99]. In the U.S., St Johnswort is distributed from Minnesota south to central Texas, east to the Atlantic Coast, and west to the northern Pacific coaSt Plants database provides a state distribution map of St Johnswort.

St Johnswort was likely introduced to North America multiple times [121]. According to Sampson and Parker [154], who review its history of introduction in North America, the 1st recorded occurrence of St Johnswort in North America was from Pennsylvania in 1793. St Johnswort was established in many western states by the early 1900s. The majority of St Johnswort infestations at that time occurred in 2 regions: the western coastal region, including northern California, western Oregon, and western Washington; and the Interior West, including northeastern Oregon, eastern Washington, northern Idaho, and northwestern Montana [78,142]. By 1945, St Johnswort infested about 2.5 million acres (1 million ha) in California, and about 1.2 million acres (500,000 ha) in Idaho, Oregon, and Washington [177]. In central North America, St Johnswort never reached the densities observed in the West, likely because cropland habitat is not ideal for St Johnswort [121].

St Johnswort population levels were dramatically reduced following a successful biological control program begun more than 50 years ago in heavily infested regions in the western U.S. [93,177]. According to Piper [143], in other areas many St Johnswort populations are still increasing in size, even where biological control organisms are present, while others have remained relatively static. A reliable published estimate of the amount of land presently infested by St Johnswort is not available [143]. Additionally, whether biocontrol in the West is currently as efficacious as it was initially is not well documented [121].

The following lists include vegetation types in which St Johnswort is known to be or thought to be potentially invasive, based on reported occurrence and biological tolerances to site conditions. Some habitats that may be invaded by St Johnswort following soil and/or vegetation disturbances are also included. Precise distribution information is limited, especially in central and eastern North America; therefore, these lists may not be exhaustive.

ECOSYSTEMS [66]:
FRES10 White-red-jack pine
FRES11 Spruce-fir
FRES14 Oak-pine
FRES15 Oak-hickory
FRES17 Elm-ash-cottonwood
FRES18 Maple-beech-birch
FRES19 Aspen-birch
FRES20 Douglas-fir
FRES21 Ponderosa pine
FRES22 Western white pine
FRES23 Fir-spruce
FRES24 Hemlock-Sitka spruce
FRES25 Larch
FRES26 Lodgepole pine
FRES27 Redwood
FRES28 Western hardwoods
FRES29 Sagebrush
FRES34 Chaparral-mountain shrub
FRES35 Pinyon-juniper
FRES36 Mountain grasslands
FRES37 Mountain meadows
FRES38 Plains grasslands
FRES39 Prairie

FRES41 Wet grasslands
FRES42 Annual grasslands

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

UNITED STATES

AR	CA	CO	CT	DE	GA	HI	ID	IL	IN
IA	KS	KY	LA	ME	MD	MA	MI	MN	MS
MO	MT	NE	NV	NH	NJ	NY	NC	ND	OH
OK	OR	PA	RI	SC	SD	TN	TX	VT	VA
WA	WV	WI	WY	DC					

CANADA

BC	NB	NF	NS	ON	PE	PQ

BLM PHYSIOGRAPHIC REGIONS [14]:
1 Northern Pacific Border
2 Cascade Mountains
3 Southern Pacific Border
4 Sierra Mountains
5 Columbia Plateau
6 Upper Basin and Range
8 Northern Rocky Mountains
9 Middle Rocky Mountains
10 Wyoming Basin
11 Southern Rocky Mountains
13 Rocky Mountain Piedmont
14 Great Plains
15 Black Hills Uplift
16 Upper Missouri Basin and Broken Lands

KUCHLER [107] PLANT ASSOCIATIONS:
K001 Spruce-cedar-hemlock forest
K002 Cedar-hemlock-Douglas-fir forest
K003 Silver fir-Douglas-fir forest
K004 Fir-hemlock forest
K005 Mixed conifer forest
K006 Redwood forest
K009 Pine-cypress forest
K010 Ponderosa shrub forest
K011 Western ponderosa forest
K012 Douglas-fir forest
K013 Cedar-hemlock-pine forest
K014 Grand fir-Douglas-fir forest
K016 Eastern ponderosa forest
K017 Black Hills pine forest
K018 Pine-Douglas-fir forest
K023 Juniper-pinyon woodland
K024 Juniper steppe woodland
K025 Alder-ash forest

K026 Oregon oakwoods
K028 Mosaic of K002 and K026
K029 California mixed evergreen forest
K030 California oakwoods
K033 Chaparral
K034 Montane chaparral
K035 Coastal sagebrush
K036 Mosaic of K030 and K035
K047 Fescue-oatgrass
K048 California steppe
K050 Fescue-wheatgrass
K051 Wheatgrass-bluegrass
K055 Sagebrush steppe
K056 Wheatgrass-needlegrass shrubsteppe
K063 Foothills prairie
K073 Northern cordgrass prairie
K074 Bluestem prairie
K082 Mosaic of K074 and K100
K093 Great Lakes spruce-fir forest
K095 Great Lakes pine forest
K098 Northern floodplain forest
K099 Maple-basswood forest
K100 Oak-hickory forest
K101 Elm-ash forest
K102 Beech-maple forest
K103 Mixed mesophytic forest
K104 Appalachian oak forest
K106 Northern hardwoods
K109 Transition between K104 and K106
K111 Oak-hickory-pine
K112 Southern mixed forest

SAF COVER TYPES [59]:
5 Balsam fir
14 Northern pin oak
16 Aspen
17 Pin cherry
18 Paper birch
19 Gray birch-red maple
20 White pine-northern red oak-red maple
21 Eastern white pine
25 Sugar maple-beech-yellow birch
26 Sugar maple-basswood
27 Sugar maple
28 Black cherry-maple
37 Northern white-cedar
39 Black ash-American elm-red maple
46 Eastern redcedar
50 Black locust
52 White oak-black oak-northern red oak
53 White oak

55 Northern red oak
60 Beech-sugar maple
63 Cottonwood
107 White spruce
108 Red maple
109 Hawthorn
110 Black oak
210 Interior Douglas-fir
212 Western larch
213 Grand fir
215 Western white pine
217 Aspen
218 Lodgepole pine
220 Rocky Mountain juniper
221 Red alder
222 Black cottonwood-willow
223 Sitka spruce
224 Western hemlock
225 Western hemlock-Sitka spruce
226 Coastal true fir-hemlock
227 Western redcedar-western hemlock
228 Western redcedar
229 Pacific Douglas-fir
230 Douglas-fir-western hemlock
231 Port-Orford-cedar
233 Oregon white oak
234 Douglas-fir-tanoak-Pacific madrone
235 Cottonwood-willow
237 Interior ponderosa pine
238 Western juniper
239 Pinyon-juniper
243 Sierra Nevada mixed conifer
244 Pacific ponderosa pine-Douglas-fir
245 Pacific ponderosa pine
246 California black oak
247 Jeffrey pine
248 Knobcone pine
249 Canyon live oak
250 Blue oak-foothills pine
255 California coast live oak

SRM (RANGELAND) COVER TYPES [158]:
101 Bluebunch wheatgrass
102 Idaho 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

202 Coast live oak woodland
203 Riparian woodland
204 North coastal shrub
205 Coastal sage shrub
206 Chamise chaparral
207 Scrub oak mixed chaparral
208 Ceanothus mixed chaparral
209 Montane shrubland
210 Bitterbrush
214 Coastal prairie
215 Valley grassland
216 Montane meadows
301 Bluebunch wheatgrass-blue grama
302 Bluebunch wheatgrass-Sandberg bluegrass
303 Bluebunch wheatgrass-western wheatgrass
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
313 Tufted hairgrass-sedge
314 Big sagebrush-bluebunch wheatgrass
316 Big sagebrush-rough fescue
317 Bitterbrush-bluebunch wheatgrass
318 Bitterbrush-Idaho fescue
319 Bitterbrush-rough fescue
322 Curlleaf mountain-mahogany-bluebunch wheatgrass
323 Shrubby cinquefoil-rough fescue
401 Basin big sagebrush
402 Mountain big sagebrush
403 Wyoming big sagebrush
404 Threetip sagebrush
405 Black sagebrush
406 Low sagebrush
407 Stiff sagebrush
408 Other sagebrush types
409 Tall forb
411 Aspen woodland
412 Juniper-pinyon woodland
415 Curlleaf mountain-mahogany
419 Bittercherry
421 Chokecherry-serviceberry-rose
422 Riparian
601 Bluestem prairie
612 Sagebrush-grass
801 Savanna
802 Missouri prairie
803 Missouri glades
804 Tall fescue
805 Riparian

HABITAT TYPES AND PLANT COMMUNITIES:
St Johnswort is treated by many authors as a grassland plant, occurring in pastures, meadows, and rangelands. It is especially invasive in "low condition range" [116]. However, St Johnswort is also common in many forested areas in North America, and may occur in open forests, natural clearings, or within forests where canopy cover has been reduced or removed by disturbances (e.g. fire, logging, road construction) (see Site Characteristics and Successional Status). Even in forested areas where St Johnswort is not found in the aboveground vegetation, it may occur in the soil seed bank and establish after disturbance (see Seed banking).

In the **Pacific Northwest**, St Johnswort occurs in a range of habitats and plant communities, including forest, woodland, rangeland, and prairie communities. In forested areas, St Johnswort is commonly associated with disturbances such as roads, logging, grazing, and fire. It is found in various stages of succession in unmanaged, naturally regenerated, closed-canopy forests in the Douglas-fir/western hemlock (*Pseudotsuga menziesii/Tsuga heterophylla*) zone of western Oregon and Washington and northwestern California [153,162] (see Successional Status). Other major tree species associated with areas of St Johnswort infestation include grand fir (*Abies grandis*), western redcedar (*Thuja plicata*), bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*) [189]. Even on sites where St Johnswort does not occur in the aboveground vegetation, St Johnswort seeds may be present in the seed bank, as was observed in a dense, closed-canopy forest dominated by Douglas-fir, western hemlock, and Sitka spruce (*Picea sitchensis*) on the Olympic Peninsula, Washington [76] (see Seed banking for additional examples).

St Johnswort occurs in parts of the Quillayute Prairie along the coastal plain of the western Olympic Peninsula, Washington, that are dominated by bracken fern (*Pteridium aquilinum* var. *pubescens*). It may occur in similar prairies within the Sitka spruce zone along the coasts of Washington and Oregon [63]. On the Willamette Floodplain Research Natural Area in western Oregon, 2 major plant communities occur. One dominates slightly elevated mounds and is marked by tall, dense sweetbriar rose (*Rosa eglanteria*), St Johnswort, and many other nonnative species. The other occurs in depressed intermounds and is dominated by shorter but also dense sweetbriar rose, tufted hairgrass (*Deschampsia cespitosa*), and many native species with wetland affinities [169]. St Johnswort occurs among tufted hairgrass, witchgrass (*Panicum capillare*) and nonnative species such as colonial bentgrass (*Agrostis capillaris*), sweet vernalgrass (*Anthoxanthum odoratum*), and hairy catsear (*Hypochaeris radicata*) on another wetland prairie site in Oregon's Willamette Valley [198].

In the interior valleys (between the Cascade and Coast ranges) of western Oregon and Washington, St Johnswort occurs in grasslands and oak woodlands among species such as Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), sweetbriar rose, Himalayan blackberry (*Rubus discolor*), poison-oak (*Toxicodendron diversilobum*), Douglas hawthorn (*Crataegus douglasii*), scotchbroom (*Cytisus scoparius*), and creeping bentgrass (*Agrostis stolonifera*) [40,63,175,180]. In grasslands there is a high proportion of nonnative species, with many nonnative annual grass dominants, such as medusahead (*Taeniatherum caput-medusae*) [63].

In the **Interior West** region, St Johnswort is common in the ponderosa pine (*Pinus ponderosa*) zone in eastern Oregon and Washington, where heavy grazing has reduced native grasses such as Idaho fescue (*Festuca idahoensis*), and dominance has shifted to nonnative species such as cheatgrass (*Bromus tectorum*), Dalmatian toadflax (*Linaria dalmatica*), St Johnswort [49], and rush skeletonweed (*Chondrilla juncea*) [137]. Similarly, where St Johnswort occurs in forest zones in Idaho it is most common in open ponderosa pine and in logged and burned areas in Douglas-fir, western redcedar-western hemlock, and fir-spruce (*Abies-Picea* spp.) zones [39,178]. In the Lochsa River area in north-central Idaho, St Johnswort occurs on sites that were previously coniferous forest types (Douglas-fir, grand fir, ponderosa pine, western hemlock, and western redcedar) until burned in 1919 and 1934. Sites are now dominated by a variety of shrubs and herbaceous species. For complete species lists see [92,115,134].

In the Blue Mountains of northeastern Oregon and southeastern Washington, St Johnswort occurs with

Kentucky bluegrass (*Poa pratensis*), Fendler threeawn (*Aristida purpurea* var. *longiseta*), cheatgrass, Japanese brome (*Bromus japonicus*), and rattlesnake brome (*B. briziformis*) on gently sloping benches formerly dominated by Idaho fescue [94,95]. In northern Idaho St Johnswort infestations occur on grasslands that were once dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue, and/or Sandberg bluegrass (*Poa secunda*) and are now dominated by nonnative annual grasses, including several brome species (*Bromus* spp.) [177]. At Garden Creek Ranch preserve in Idaho, St Johnswort occurs in large and small populations in bluebunch wheatgrass, Idaho fescue, and snowberry-rose (*Symphoricarpos-Rosa* spp.) communities, and in areas where it may impact populations of Spalding's silene (*Silene spaldingii*), a threatened species [149].

In northwestern Montana, St Johnswort occurs among sagebrush (*Artemisia* spp.) and Idaho fescue grasslands, and on disturbed forest sites dominated by Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir, western white pine (*Pinus monticola*), western redcedar, grand fir, spruce, and/or alder (*Alnus* spp.) [189]. St Johnswort occurred on several sites infested with sulphur cinquefoil surveyed by Rice [150] in western Montana in 1991 and 1992. In 1939, St Johnswort was listed as occurring along Bear Creek in Glacier National Park; the author suggests that it was "possibly of recent introduction to the park" [120].

In **California**, St Johnswort is most commonly an invader of California prairies and annual grasslands [15,85]. It also occurs along roadsides in many forest types such as those characterized by ponderosa pine, Pacific madrone (*Arbutus menziesii*), grand fir, bigleaf maple, and giant chinquapin (*Chrysolepis chrysophylla*), and St Johnswort infestations may extend into the forests in these areas [189]. St Johnswort occurs along edges (e.g. roads, streams, etc.) at Dye Creek and Vina Plains preserves in California, in grasslands, riparian areas, blue oak (*Quercus douglasii*) woodlands, and vernal pool complexes [149].

In **central North America**
St Johnswort is found primarily in fields and along roadsides and ditches, as well as moist ravines (or low, moist ground), prairies, pastures, open woods, and rangelands. It is not considered as serious a problem here as in the Northwest [9,69,163,170]. St Johnswort is widespread in the Missouri Ozarks and sometimes common and abundant in open woods, fields, and "waste areas," as well as streambanks and low ground [44].

In Michigan, St Johnswort is commonly found on abandoned agricultural fields, often among other nonnative species [57,61]. At Kitty Todd preserve in Ohio, St Johnswort occurs in mesic sand prairie, Midwest sand barrens, and black oak/lupine (*Quercus velutina*/*Lupinus* spp.) barrens, and may impact populations of rough false pennyroyal (*Hedeoma hispidum*), a threatened species [149].

Literature is sparse for St Johnswort occurring in **eastern North America**. However, it seems that St Johnswort occurs in many old field and forest types. It occurs in several management units at Gettysburg National Park in Pennsylvania. See Yahner and others [202] for a list of dominant species. St Johnswort occurs in both burned and unburned goldenrod-oatgrass (*Solidago-Danthonia* spp.) fields, and quaking aspen (*Populus tremuloides*) groves in south-central New York state [171]. It also occurs with woodsorrel (*Oxalis* spp.) and mountain maple (*Acer spicatum*) in a beech-maple-birch/aster (*Fagus-Acer-Betula/Aster* spp.) association in southern New York [196].

On Montague Plain in central Massachusetts, St Johnswort occurred only on plots that had been previously plowed. Vegetation types on these sites are characterized by high frequency and cover of forbs and graminoids, especially little bluestem (*Schizachyrium scoparium*), and including numerous weedy or early successional species. Shrubs characteristic of old fields such as white meadowsweet (*Spiraea alba* var. *latifolia*), and common juniper (*Juniperus communis*) are also frequent [133]. St Johnswort occurs in various plant communities on Nantucket, Cape Cod, and Martha's Vineyard. It is most common in grasslands, especially those dominated by other nonnative species or by little bluestem. It is less common on shrub-dominated communities [55].

St Johnswort is found in cedar glades in the Big Barren Region of Kentucky in openings surrounded by eastern redcedar (*Juniperus virginiana*) thickets [12]. In the Roanoke River Basin of North Carolina's coastal plain, St Johnswort is found at the edge of hardwood forests dominated by many tree species such as white oak (*Quercus alba*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), sweetgum (*Liquidambar styraciflua*), and a mix of hickories (*Carya* spp.). Flowering dogwood (*Cornus florida*), blueberries (*Vaccinium* spp.), and grapes (*Vitis* spp.) are common understory dominants [64].

In **Canada**, St Johnswort occurs in old fields, pastures, abandoned hayfields, and similar habitats. The frequency of occurrence of St Johnswort and associated species in several habitats in Nova Scotia is given by Crompton and others [45].

Near Ottawa, Ontario, St Johnswort is occasionally found after fires in alvar ecosystems (naturally open areas) surrounded by forested areas dominated by northern white-cedar (*Thuja occidentalis*), quaking aspen, balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and eastern white pine (*Pinus strobus*) [37,38]. In an old-growth, temperate deciduous forest in Quebec, St Johnswort was present in the seed bank, although absent from aboveground vegetation. Overstory dominants there included sugar maple (*Acer saccharum*), striped maple (*Acer pensylvanicum*), American beech, white ash (*Fraxinus americana*), northern red oak (*Quercus rubra*), eastern hophornbeam (*Ostrya virginiana*), basswood (*Tilia americana*), paper birch (*Betula papyrifera*), mountain maple, chokecherry (*Prunus virginiana*), and yellow birch (*B. alleghaniensis*) [114]. St Johnswort occurs on Pelee Island, Ontario, in the western Lake Erie archipelago. Dominant vegetation includes chinkapin oak (*Quercus muehlenbergii*), big bluestem (*Andropogon gerardii* var. *gerardii*), blue ash (*Fraxinus quadrangulata*), eastern redcedar, white oak, hackberry (*Celtis occidentalis*), and shagbark hickory (*Carya ovata*) [103].

For examples of plant communities in which St Johnswort is commonly invasive in Australia, see these publications: [20,34,41].

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Hypericum perforatum

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GENERAL BOTANICAL CHARACTERISTICS:
The following general description is a synthesis of botanical characteristics presented by several authors in North American florae [9,16,52,67,69,89,109,168], ecological studies [22,41,154,178], and literature reviews [34,45,78,139] from Australia and North America. This description provides characteristics of St Johnswort that may be relevant to fire ecology, and is not meant for identification. Keys for identification are available (e.g. [69,89,109,127,187]).

St Johnswort is an herbaceous, erect, perennial forb, up to 5 feet (1.5 m) tall, but commonly 1 to 3 feet (0.3-1 m) tall, depending on genotype and site type. One to several (up to 30) stems arise from a woody root crown. Stems are woody at the base, leafy, and many-branched, mostly in the upper half. Leaves are 0.6 to 1.2 inches (1.5-3 cm) long and 1.5 to 5 mm wide. Flowers are numerous (generally 25-100 per stem), about 0.8 inch (2 cm) in diameter, and occur in terminal clusters (open, flat-topped, cymes). The fruit is a sticky, many-seeded, 3-celled capsule, 5 to 10 mm long. Seeds are about 1 mm long. Following senescence of St Johnswort stems in mid- to late summer, procumbent growth occurs in response to increased soil moisture in fall or winter. This growth consists of numerous branched, densely leaved, non-flowering stems up to 1 foot (0.3 m) long (see Seasonal Development).

Roots:

A single St Johnswort plant consists of 1 or many aerial crowns attached to a system of vertical and lateral roots. Several authors describe a taproot in St Johnswort (e.g. [34,89,109]), and vertical roots are generally said to extend to depths of 2 to 5 feet (0.6-1.5 m), depending upon the nature of the soil and its moisture content. Lateral root growth may be extensive, and occurs 0.5 to 3 inches (1-8 cm) below the soil surface. In autumn and/or spring, or following plant injury, lateral roots produce buds from which new crowns develop. With the decay of connecting roots, new crowns become independent plants [41]. These young sprouts may be so numerous that they "mat the ground near the parent plant" [154].

Sampson and Parker [154] provide a detailed cellular anatomy of St Johnswort leaves, stems, seeds, and roots. According to Crompton and others [45], Esau (1960) describes a protective tissue of suberized cells called polyderm which protect the roots of St Johnswort plants. Harris and Clapperton [83] observed St Johnswort plants collected from natural Canadian field infestations, and found 31% (± 8%) of St Johnswort roots were infected with vesicular-arbuscular mycorrhizal fungi. Klironomos [104] found that St Johnswort became infected by an arbuscular mycorrhizal (AM) fungus when inoculated under experimental conditions. St Johnswort seedlings inoculated with AM fungi were better able to tolerate harsh environmental conditions, but not necessarily to compete with mature St Johnswort plants for resources [131] (see Seedling establishment/growth).

Growth habit/stand type:

The growth habit of St Johnswort (one to several crowns attached to a system of vertical and lateral roots) makes the designation a single St Johnswort "plant" ambiguous. Clark [41] uses "crown" to designate a single plant in her writing. Where it is not specified, it may be assumed that when authors refer to a single St Johnswort "plant", they are indicating a single crown, and not multiple crowns sharing a common root system. This review will assume that and use this designation.

Crown and stem density of St Johnswort may be affected by many variables. Stem production in St Johnswort may be affected by rainfall pattern, insect defoliation, and site factors ([22] and references therein), with St Johnswort population fluctuations and dynamics driven by complex interactions of several stress factors (e.g. shallow, rocky soils, shading, drought, herbivory), and/or positive factors such as good rainfall years [22]. For example, deep soils favor development of vertical roots and long-term crown survival, while shallow soils tend to support St Johnswort populations with more lateral roots, root sprouts, and shorter-lived crowns [22,41,45]. Australian authors describe 2 types of St Johnswort stands in greater detail [22,41]. Buckley and others [24] suggest that site-to-site differences described by these authors are less important to individual plant life histories than the differences between plants in shaded and open sites, and differences between individual plants within a site (also see Successional Status).

Accounts in North American literature suggest that St Johnswort typically forms dense stands in many areas in the West [45,78]. Harris [78] describes a "typical" St Johnswort near Colville, Washington, as dense, "almost to the exclusion of other herbaceous vegetation." Sampson and Parker [154] describe dense St Johnswort stands in California with winter annuals in the understory. In contrast, in the central U.S. [69,170] and eastern Canada [45] St Johnswort occurs as small infestations or as individual plants.

Variation:

St Johnswort exhibits a high degree of phenotypic and genotypic variation, particularly among populations. Several studies comparing characteristics of St Johnswort among populations in California, Oregon and Montana, found strong regional differences in chemical (hypericin and psuedohypericn content) and morphological (gland density, leaf area, stem length, leaf length/width ratio) characteristics [159,189,190]. St Johnswort exhibits genetic variation with respect to morphological variation and herbivore resistance [24,35,122].

Early reviews cite common garden experiments by Pritchard (1958,1960) as evidence that introduced populations of St Johnswort are taller and more competitive than populations from areas where it is native or areas where it is not "weedy" [45,130]. Conversely, when Vilà and others [185] tested the relative competitive ability of native St Johnswort from Europe and introduced St Johnswort from central and western North America, they found St Johnswort plants from the introduced range were neither uniformly larger nor better interspecific competitors than St Johnswort plants from its native range. Additionally, Maron and others [121] performed reciprocal common garden experiments and molecular analysis of genetic variation in St Johnswort, and found that introduced St Johnswort plants were neither consistently larger nor more fecund than natives across all gardens. Both native and introduced plants exhibited substantial phenotypic plasticity, and had greater genetic variability among populations than within populations or among regions. Latitudinally based clines in fitness in almost all gardens suggest that both native and introduced St Johnswort have adapted to broad-scale abiotic conditions in their current range. The authors conclude that the patterns observed suggest that many St Johnswort populations were founded by individuals that were not pre-adapted to the latitude (and hence climatic conditions) of introduction. Plants within these populations appear to be evolving in response to current conditions experienced in their recipient community. Their results "support the contention that introduced plants can undergo contemporary evolution, and that adaptive evolution may be one of several key mechanisms enabling exotics to succeed in recipient communities" [121].

RAUNKIAER [146] LIFE FORM:
Hemicryptophyte
Geophyte

REGENERATION PROCESSES:
St Johnswort reproduces by seed and by sprouting from lateral roots and root crowns.

Breeding system: St Johnswort is a facultative apomict. Reproduction of St Johnswort throughout Europe is 97% apomictic. St Johnswort pollen undergoes normal meiosis (Robson 1968, as cited by [34]).

Pollination: There is evidence of both self-pollination [9,45,135] and pollination by a variety of insects [9,45] in St Johnswort. Flowers self-pollinated in greenhouse studies developed equally well as those that were cross-pollinated. Field observations in Canada indicated that domestic and wild bees preferred clover (*Trifolium* spp.) and bird vetch (*Vicia cracca*) over St Johnswort [45]. In a mid-successional, "prairie-like grassland" in an abandoned field in southeastern Michigan, St Johnswort was "heavily visited" by at least 35 bee species [57].

Seed production:

Estimates and measurements of seed production for St Johnswort are variable, but range from about 15,000 to 34,000 seeds per plant on average [45,154,178]. Variation in seed production may result from site factors, seasonal growth conditions, competition, and/or herbivory.

In St Johnswort population studies on 4 contrasting sites in Australia, seed production varied from none to 200,000 seeds per m^2
over 7 years. The median number of years in which fruit were produced on tagged plants varied from 1 to 3 years, with a maximum of 3 to 7 flowering periods at individual sites over 7 years. A typical pattern was for years of flowering to be interspersed with years in which nonflowering stems were produced (usually drought years), or in which seed production was prevented by insect defoliation. Some crowns never produced fruit, even though they survived for up to 7 years [22].

Salisbury (1942) estimated 26,000 to 34,000 seeds per St Johnswort plant per year in England [178]. Six plants collected in Nova Scotia had 400 to 502 seeds per capsule, with an average of 451. The number of capsules per plant (of 17 plants) ranged from 70 to 76, with an average of 73, giving an estimated total of 33,000 seeds per plant [45]. Sampson and Parker [154] gave a "conservative estimate" of 15,000 seeds on a fully developed St Johnswort plant in California. Tisdale and others [178] examined 512 St Johnswort plants on 6 sites selected to represent the range of conditions within a grassland zone on the Clearwater River in Idaho. They found an average of 69 $\pm$ 9.8 seeds per capsule, 94 $\pm$ 12.2 capsules per stalk, and 3.6 $\pm$ 0.4 flower stalks per plant, estimating an average seed production of 23,350 seeds per plant [178].

Tisdale and others [178] found a high degree of variability in seed production during their field studies in Idaho, with seed production per plant ranging from a few thousand to nearly 100,000. Although not tested, they speculate that this variation could result from site factors, seasonal growth conditions, and/or intraspecific competition. They cite evidence presented by Evanko (1953) in which the number of seeds per St Johnswort plant was much greater in peripheral than in centrally located plants in dense stands of St Johnswort in northeastern Washington [178]. A comparison of annual seed production in St Johnswort in New South Wales, Australia, indicated several differences between 2 years with very different rainfall. Data collected were as follows [34]:

Year	1973	1982
Rainfall (mm)	1,013	235
Seeds per capsule	70	30
Capsules per flowering stem	150	35
Flowering stems per m^2	250	100
Seeds per m^2	2.6×10^6	1×10^5
Seeds per ha	26.25×10^9	1.50×10^8

Seed dispersal: St Johnswort seed can be dispersed by wind, water, humans, and other animals.

Because St Johnswort seeds have no devices to facilitate dispersal by wind, it has generally been assumed that animal or water transport are the main dispersal agents for St Johnswort seed. Tests conducted by Tisdale and others [178] indicate, however, that wind cannot be ignored as a dispersal agent. Seed traps distributed 10, 20, and 30 feet (3, 6, and 9 m) downwind from the nearest St Johnswort plants collected an average of 148, 27, and 7 seeds during the period when most seed at these sites was shed [178]. Walker [189] observed St Johnswort infestations at Kilby Ranch in Oregon over 3 years following a prescribed burn, and suggested that St Johnswort seeds may have been dispersed as far as 0.3 mile (0.5 km) by wind, although this was not tested. This St Johnswort population continues to expand in the direction of prevailing winds [189].

Waterways may also be important dispersal vectors for St Johnswort seed. Comes and others [42] report 7% germination, and 73% of St Johnswort seeds remaining firm after 5 years of storage in fresh water. In another study, germination rates of St Johnswort seed increased with length of time seed was immersed [154]. Similarly, Parsons and Cuthbertson [139] suggest that much of the early spread of St Johnswort in Australia occurred along streams when many infested areas were extensively dredged and sluiced for gold.

Birds and mammals may also aid St Johnswort seed dispersal. The seed is borne in sticky capsules that may adhere to the feet and bodies of birds and mammals ([81] and references therein). It is also suggested that the sticky exudate from the capsule may adhere to the seedcoat and thus aid in seed dispersal [41], or that the seedcoat itself is sticky and/or gelatinous [34,45]. Heavy stands of St Johnswort often occur along livestock driveways and animal trails [34,78,124,139,154]. Some reviews [34,81,139] also suggest that St Johnswort seed remains viable after passing through animals, and may thus be dispersed in the feces of animals that consume it. There is, however, no experimental evidence to support this.

Roads and railroads are also vectors of St Johnswort spread, as seed may be dispersed by humans on vehicles, equipment, and in agricultural products [34,78,139]. Once pioneer plants become established, the stand of St Johnswort may spread to adjoining plant communities.

Seed banking: Some authors suggest that seeds of *Hypericum* species remain viable in the soil for periods longer than 50 years ([191] and references therein). Evidence from both laboratory and field studies suggests that St Johnswort seed may persist in the soil seed bank for several years, although the ultimate longevity is unclear [41,42,78,81,178]. The combination of a high rate of production and persistence of seed in St Johnswort suggests that any site which has supported a population of St Johnswort for even a few years has a high potential for St Johnswort seedling production for several years after mature plants are removed [81]. Additionally, several studies provide evidence that viable St Johnswort seeds occur in the soil seed bank in areas where mature plants do not occur or occur only at some distance from the sampled sites [76,81,111,114,117,176].

Reports of St Johnswort seed viability following dry storage in the laboratory indicate 94% germination after 5 years [42], and 50% germination after 16 years of storage [178]. Several researchers indicate that St Johnswort seed remains viable under field conditions for several years [41,78,81,178]. Observations by Clark [41] indicated that St Johnswort seeds remain viable in the soil for at least 6 years at field sites in Australia. Bellue (1945, as cited by [78,178]) suggests that St Johnswort seed retains viability in the soil for 10 years in California. Harris and Gill [81] estimate St Johnswort seed longevity at 30 years or more in pine (*Pinus* spp.) plantations in Australia. Tisdale and others [178] tested viability of St Johnswort seed buried in clay pots at 3 depths over a 3-year period in silt loam soil near Lewiston, Idaho, where mean annual precipitation is about 14 inches (356 mm). Results are as follows [178]:

Number of years buried	Germination (%)		
	0.5-inch depth	1-inch depth	3-inch depth
1	20.6	27.3	25.2
2	30.6	42	62
3	9.6	45	52

These results indicate that a considerable proportion of St Johnswort seed may retain viability for at least 3 years, particularly if buried 1 inch (2.5 cm) or deeper [178].

Several seed bank studies indicate the presence of St Johnswort seed in areas where mature plants are rare, do not occur, or occur only at some distance from the sampled sites. Harris and Gill [81] suggest that when a pine plantation (or a forest) reaches stand closure, St Johnswort may disappear from aboveground vegetation, but remain at the locality in the form of seed in the soil. On a "high-quality" native prairie site in western Oregon, St Johnswort seed was present in the soil seed bank, although St Johnswort plants were not abundant in the prairie [197]. St Johnswort seedlings emerged from a few soil samples taken from 1 site in a dense, closed-canopy forest dominated by Douglas-fir and western hemlock on the Olympic Peninsula, Washington, although St Johnswort was not present in aboveground vegetation [76]. In a grassland remnant surrounded by second-growth woodlands and agricultural fields in a limestone prairie in central Pennsylvania, St Johnswort seed was present in the soil seed bank under grassland and edge vegetation, but not under forest vegetation. St Johnswort was not present in the vegetation aboveground in any of the vegetation types [111]. In an old-growth, temperate deciduous forest in Quebec, St Johnswort was present in the seed bank at 1 of 31 study plots, although it was not present in aboveground vegetation at any of the 31 plots. The authors speculate that St Johnswort seed may have come from surrounding developed areas [114]. St Johnswort seedlings emerged from soil samples from 9 of 13 forest and plantation sites of various ages (from a 5-year-old eastern white pine stand to a 47-year-old eastern white pine plantation) at Harvard Forest, Massachusetts. St Johnswort was not present in aboveground vegetation on these sites, but was present on open field sites nearby, where it was also present in the seed bank [117]. Similar observations were made on sites in Italy [118], England [191], and several other European sites not discussed in this review.

Other studies provide evidence that viable St Johnswort seeds occur in the soil seed bank as indicated by postdisturbance seedling establishment. One year after clearcutting and site preparation (scraping away surface organic layers with a bulldozer) in a 100-year-old eastern white pine stand in northwestern Connecticut, St Johnswort seedlings were frequent (5 to 15 seedlings in about 2,900 m^2) to abundant (over 100 seedlings in about 2,100 m^2). It is unclear if and where mature St Johnswort plants occurred in the area of the clearcut, or how long the seeds may have been buried [51]. Thysell and Carey [176] examined 1- and 3-year responses of understory plants to variable-density thinning of 55- to 65-year-old stands of Douglas-fir on Fort Lewis Military Reservation, Washington. St Johnswort was absent in control stands, but established and increased significantly (P=0.014) after thinning, and continued to spread at post-thinning year 3 [176].

The information provided in these studies is insufficient to indicate how long St Johnswort seeds retain viability under various field conditions. They do, however, indicate a high likelihood of St Johnswort establishment from buried seed following disturbance (logging, thinning, burning, road construction, etc.). Managers should be prepared for St Johnswort establishment following activities that disturb soil or open the canopy in areas where St Johnswort may have been present or is nearby.

Germination:

Considering the large amount of seed produced by St Johnswort, it is important to know when, under what conditions, and what percentage may be expected to germinate. St Johnswort seed dormancy and germination requirements are complex, and seem to be affected by age and source of seed, moisture, temperature, light, nutrients, disturbance, and interactions of these factors.

Several authors have tested for dormancy in St Johnswort seeds, with variable results. Cashmore (1939, as cited by [32]) found St Johnswort seed needed an after-ripening period of 4 to 6 months before it became germinable, and 12 months for it to reach maximum germination capacity. Clark [41] found germination in 9- to 12-month-old St Johnswort seed was erratic and low, with maximum germination of 25%. Sampson and Parker [154] reported germination percentages varying from 5.5% to 63.5% for duplicate seed lots tested over a 40-day period. No indication of the age of these seeds or of the period elapsed since ripening was given. Tisdale and others [178] found large differences in germination (36.2%-84.2%) among sites in Idaho in St Johnswort seed collections of the same year. They then collected St Johnswort seed from 1 site at about 1-week intervals from mid-September to mid-October and tested it for germination within 3 to 6 days of collection. The earliest collections averaged 43% germination, and germination rates increased over later collection dates, reaching a maximum of 58%. Samples tested for germination within a few days of collection took 2 to 5 days longer to begin germinating than did lots stored for 3 to 4 months before testing germination [178]. St Johnswort seed that overwintered in capsules in Nova Scotia, had a lower germination compared to seed stored at 36 °F (2 °C) for 2 years [45]. Reports such as these and the following suggest a dormancy in St Johnswort seeds that may be broken by washing, heat treatment, light, or an after-ripening period.

Field observations by Clark [41], particularly a flush of St Johnswort seedlings in a mature St Johnswort stand after 3 weeks of heavy rain, suggested the presence of a water-soluble inhibiting substance in St Johnswort litter or seed capsules. A germination test was made, using seeds washed with several lots of rainwater. After 7 days, more washed seed germinated (69%) than unwashed seed (34%), washed seed plus leaf extract (44%), and washed seed plus capsule extract (5%). Total germination after 28 days was lower for washed seed plus capsule extract (23%) than for any other treatment (mean 77%). Clark concluded that capsule exudate on St Johnswort seed explained much of the inhibition of germination. Sampson and Parker [154] also reported stimulation of germination after immersion of St Johnswort seed in water for 5 to 20 days, with germination percentages of up to 74%, compared to about 44% germination in control lots. Campbell [32] found that percentage germination of both new (1-6 months old) and old (9 years) St Johnswort seeds was significantly improved ($p<0.01$) by washing. Crompton and others [45] report a seedling flush often occurs in ground blueberry (*Vaccinium myrsinites*) fields treated with hexazinone, which may be explained by washing of the seeds by the chemical.

Sampson and Parker [154] report stimulation of St Johnswort seed germination after brief (5-60 minute) exposures to temperatures of 212 °F (100 °C) and 260 °F (127 °C). Germination percentages of up to 81% were obtained with heat treatments, while germination of control lots averaged 44% (see Discussion and Qualification of Fire Effect for more details) [154]. Conversely, hot water (129 °F (54 °C)) immersion for 5 minutes did not break dormancy in St Johnswort seed, and depressed germination of some seed lots. Hot water immersion for 15 minutes killed all seeds from all locations. Seeds were washed in tap water for 5 minutes before hot water immersion [32].

Precise temperature requirements for germination of St Johnswort seeds are unclear, as seed source, age of seed, and exposure to conditions that may release seed dormancy are important variables to consider, and not consistently or comprehensively accounted for in St Johnswort seed germination studies. For example, Campbell [32] found different germination and dormancy characteristics in St Johnswort seed from different sites and different ages. In general, St Johnswort seems to germinate during warm months when adequate moisture is present. Germination may be limited by temperature extremes and promoted by fluctuating temperatures. See these references [32,34,41,174] for further discussion on temperature requirements for St Johnswort seed germination.

While St Johnswort seeds did not germinate in the greenhouse in the dark [174], buried seed may sometimes germinate. Tisdale and others observed limited germination (9% at 0.5 inch, 5% at 1 inch, 1% at 3 inches) from seed buried in the field at various depths. However, no seedlings emerged from 1- or 3-inch (2.5 or 8 cm) depths. A few seedlings emerged from 0.5-inch (1 cm) depth, but none survived [178]. Bosy and Reader [18] found that a covering of grass litter significantly ($p<0.05$) reduced germination and shoot extension of St Johnswort in the laboratory. Several studies indicate St Johnswort seedling emergence following ground cover or canopy removal and/or soil disturbance [51,147,176]. Campbell [32] found the respective percentage of St Johnswort seedling emergence from under 0, 2, 4, and 8 mm of soil was 57%, 8%, 1% and 0. The author suggests this may be due more to physical impediment than to a lack of light, but this was not tested.

Conclusion/field implications: Clark [41] suggests that the apparent dormancy of St Johnswort seed is determined primarily by the sticky exudate of the seed capsule, which adheres to the seed coat and aids in seed dispersal, and secondarily by the immediate physical environment of the seed in the soil. As a result, germination is delayed until the capsule exudate is washed or worn away, and/or temperature, light, and moisture conditions are appropriate for germination. According to Clark [41] favorable temperature and moisture conditions for germination occur in the field only for short periods of 1 to 2 weeks, and rarely for as long as 4 weeks. Mass germination events, as observed by Sampson and Parker [154] in California, by Walker [189] in Oregon, and by Briese and Clark [22,41] in Australia, may be explained by events and conditions that coincide to favor germination of the previously dormant St Johnswort seed bank.

Seedling establishment/growth:

The conditions favorable to St Johnswort seed germination and seedling emergence are apparently exacting. As a result, undisturbed, dense stands of St Johnswort have few seedlings, St Johnswort seedlings only occasionally appear in large numbers [154], and only a small percentage of emergent seedlings establish and grow. For example, less than 1% of 40,000 St Johnswort seedlings that emerged after a stand of mature St Johnswort plants was killed by insects survived after 3 years on a site in Victoria, Australia [41]. Challenges to seedling establishment and growth include St Johnswort seedling size, slow growth rate, intra- and interspecific competition, and moisture stress.

Seedlings of St Johnswort are very small and grow slowly compared to seedlings of many associated species. This slow growth renders St Johnswort seedlings susceptible to competition for light, nutrients, space, and moisture from mature St Johnswort plants and other species [32]. Greenhouse and laboratory experiments indicate that St Johnswort seedling growth is improved when inoculated with arbuscular mycorrhizal fungi, but that the positive growth response is not apparent when seedlings are grown with adult St Johnswort plants [131].

Seedling development and survival in the field were studied in Idaho at 3 sites in 1952 and 8 sites in 1953 [178]. All sites had a well-developed cover of mature St Johnswort plants, along with annual and perennial grasses and forbs. The number of St Johnswort seedlings per 0.1 m^2 sample plot averaged 57 in 1952 and 71 in 1953. Seedling mortality was extremely high both years, averaging 96% in 1952 and 99% in 1953. The critical period for seedling survival came in late July and in August, when normal precipitation was low and air and surface soil temperatures were at their maximum. Seedlings that did survive the summer drought attained a height of 2 to 4 inches (5-10 cm) above ground, and extended their roots to a depth of 12 inches (30 cm) or more. Some additional mortality of seedlings during their 1st winter was observed, especially on sites with little snow cover. Conspicuous branching of roots began in the 2nd growing season. Variability was high between sites, but had no obvious relationship to vegetation or habitat [178].

Sampson and Parker [154] reported a similar situation in northern California, where most years' seedling survival was nil, but the occurrence of favorable moisture conditions resulted in an "enormous" emergence from seed on occasional years. This results in a population growth pattern where patches of St Johnswort enlarge slowly by vegetative means, and then occasionally expand rapidly through seedling establishment to coalesce and cover large areas [154,178].

Briese [22] tracked population dynamics at 4 qualitatively diverse sites in Australia for 7 years and recorded 1 to 3 mass germination events per site during the 7 years (total of 9 events at 4 sites over 7 years). Seedling survival, however, was less than 10%. Abrupt increases in infestation densities occur as a result of seedling recruitment following conditions favorable for germination. Hence, he says, massive germination is required to substantially increase infestation density and conditions for such events are relatively rare (maximum of 3 in 7 years at 4 sites), while successful recruitment from these is even rarer (once in 7 years at 4 sites). Recruitment recorded at the study sites in 1984 seems to have occurred throughout a wide range of southeastern Australia [22].

Establishment of St Johnswort seedlings is favored by bare soil (e.g. rabbit scratches, burnt areas) and wet summers [41]. Greiling and Kichanan [71] found that St Johnswort seedling emergence was significantly higher ($p<0.01$) when plant neighbors (little bluestem and old field species) were removed. They also found that insecticide treated plots had nearly double the seedling survival rates as untreated plots, indicating a strong effect of insect herbivores on seedling survival [71]. St Johnswort seedling survival to maturity is low, unless competition is restricted or absent. Consequently, St Johnswort is a weed of disturbed areas and other sites where competition is low (e.g. eucalyptus (*Eucalyptus* spp.) forests, and hill country in Australia) [32].

Once St Johnswort plants have survived the critical 1st year, they may have an advantage over associated plants as their extensive root system develops, especially if they can grow taller than associated plants [41]. St Johnswort plants more than 1 year old may have extensive horizontal roots [154]. Neither flowers nor seeds are produced by 1st-year St Johnswort seedlings [22,78].

Asexual regeneration:

Asexual regeneration of St Johnswort from root fragments, root crown, or lateral root sprouts is reported by many workers, and in Australia some layering has also been observed from fall growth [41,178]. An individual St Johnswort plant spreads via the growth of lateral roots, thereby increasing its area concentrically [34]. Harris [78] says new St Johnswort plants originate at intervals along underground roots that may extend 3 feet (90 cm) or more from the parent plant. In northern Idaho field studies, vegetative spread was due mainly to sprouting from lateral roots a few inches below the soil surface. Tisdale and others [178] observed that vegetative propagation was stimulated by grazing, fire, defoliation (if not too severe), and shallow or very rocky soils. Clark [41] reported similar observations in Australia and stressed the relationship of poor site quality to increased vegetative propagation.

In general, plants propagated vegetatively severed connections with the parent plant fairly soon after new plants established, making it difficult to distinguish crowns developed by vegetative means from those arising as seedlings [41,178]. It was noted, however, that plants that developed from seed formed taproots with axes in a straight line with crowns, while the taproots of vegetatively propagated plants were not so aligned. A study of 6 sites, using these criteria, indicated that 46% of 208 crowns had arisen by vegetative means. It is possible that this percentage might be higher in denser stands and on poorer sites [178]. Population studies in Australia indicate the average percentage of crowns originating vegetatively is often well over 50% [22].

In greenhouse experiments, sections of St Johnswort root sprouted when buried at depths up to 2 inches (5 cm) in moist silt loam soil, but failed to sprout at greater depths. On the 4-inch (10 cm) root sections used, 2 sprouts sometimes developed [178].

SITE CHARACTERISTICS:

General:

In California, the Pacific Northwest, and the Intermountain area, where St Johnswort is most problematic, it occurs most commonly and develops best in pastures, open grasslands, abandoned fields, and disturbed places [89,136,154,178]. It occupies all slopes and aspects [154]. Observations by Walker [189] suggest that, while St Johnswort is common along roadsides in forested areas California and Oregon, populations tend to extend further from roadsides into adjacent plant communities in California than in Oregon. In forest zones in Idaho, St Johnswort is abundant only in small, localized areas in naturally open ponderosa pine forest stands or in areas where tree cover has been greatly reduced by logging, fire, or other disturbance (e.g. in Douglas-fir, western redcedar-western hemlock, and fir-spruce zones). Serious spread of St Johnswort into "well-stocked" forest stands in Idaho has been observed only in ponderosa pine [178]. Similar site characteristics are described for areas where St Johnswort is invasive in Australia [34,41], although a large proportion of infestations (estimates of 80%) occur under native eucalyptus forests (Shepherd 1983, as cited by [22]).

In Colorado, St Johnswort is locally abundant on piedmont valleys and outer foothills, but mostly kept in check by biological control insects [192,193]. In central North America, St Johnswort is found primarily in the central and eastern Great Plains and scattered westward in fields and along roadsides and ditches, as well as moist ravines (or low, moist ground), prairies, pastures, open woods, and rangeland. It is not considered as serious a problem as it is in northwestern North America [9,69,163,170]. At Matfield Green, Kansas, distribution of nonnative plants, including St Johnswort, formed a gradient from high abundance in the townsite and along truck trails, to low abundance in the surrounding prairie [56]. In Michigan, St Johnswort is abundant on fields and along roadsides and railroads, and may spread to rock outcrops, dunes, and shores [149,187]. Along the Atlantic coast from Newfoundland to northern Virginia, St Johnswort may occur in meadows, fields, between stable dunes, along marsh edges, on beaches, and along roadsides [54]. In other parts of North America, St Johnswort seems to be less invasive and is most commonly found along travel corridors (roadsides and railways) [67,77,108,127,145,199], in fields and pastures [16,67,77,100,108,127,145,152,168,199], and in "waste places" [16,77,100,108,168].

Elevation:

While temperature, precipitation, and elevation are important in influencing the spread of St Johnswort in local areas [154], relatively little information is available regarding elevational limits for St Johnswort throughout its introduced range. Some elevations of occurrence by geographic area are given as follows:

Geographic area	Elevation	Reference
CA	below 5,000 feet (1,500 m)	[89,136]
CO	5,500 feet (1,680 m)	[77]
ID	743 to 4,000 feet (226-1,220 m)	[177,178]
MT	3,000 to 5,000 feet (900-1,500 m)	[189]
NV	4,000 to 5,000 feet (1,200-1,500 m)	[100]
OR	up to 3,330 feet (1,000 m)	[160,189]
Adirondack area	2,880 feet (880 m)	[108]
Australia	below 5,000 feet (1,500 m)	[41]

St Johnswort requires a moderately warm and long growing season for completion of its life cycle [41,154]. In California, the densest and most extensive stands described in the 1930s were usually found only a few hundred feet above sea level, with 1 vigorous stand known to occur at sea level (in Humboldt County). At elevations of 4,000 feet and higher, St Johnswort stands are open and plants less vigorous than at lower altitude [154]. Tisdale [177] reports that early infestations of St Johnswort in Idaho occurred between 1,200 and 4,000 feet, (370-1,220 m) but rarely occurred above 3,500 feet (1,100 m). In Australia, the most vigorous infestations of St Johnswort occur at altitudes of about 2,000 feet (600 m) [34], and the highest altitude at which St Johnswort occurs is between 4,500 and 5,000 feet (1,400-1,500 m), where a small patch was found [41]. Clark [41] and Sampson and Parker [154] speculate that St Johnswort's absence at higher elevations is due to low temperatures and short growing seasons that would limit St Johnswort seed production and seedling survival.

Temperature: Where St Johnswort thrives in Idaho, mean monthly temperatures range from 67 to 77 °F (19-25 °C) in July and 27 to 34 °F (-3-1 °C) in January [178]. In Canada, St Johnswort occurs in the mild mesic, moderately cool boreal and cool boreal soil temperature classes (Canada Dept of Energy, Mines, and Resources 1970, as cited in [45]). St Johnswort is restricted by low temperatures at high elevations (above about 5,000 feet (1,500 m)) [41,154] and is restricted by a normal mean January temperature over 75 °F (24 °C) at lower elevations (Campbell 1977 as cited by [34]). In South Australia and Western Australia, where the growing season is short, St Johnswort grows in scattered open communities. This contrasts with the dense stands in New South Wales and Victoria (Moore and Cashmore 1942, as cited by [34]). In the northernmost part of St Johnswort's North American distribution the length of the growing season is approximately 160 days, and in the most southern portion it is 210 to 220 days [45]. In experiments performed near the northern boundary of St Johnswort's European distribution in England, Fox and others [62] found that experimental winter warming increased spring growth in St Johnswort, but had mainly negative effects on St Johnswort populations. Winter warming increased herbivory with normal rainfall or drought, but not with increased precipitation. Summer drought reduced St Johnswort's reproductive success indirectly by increasing its vulnerability to herbivorous insects [62].

Moisture:

Precise moisture requirements for St Johnswort are unclear. In Australia, St Johnswort is said to grow in areas with mean annual rainfall greater than 30 inches (760 mm) [24]. Harris [78] indicates that North American St Johnswort populations require 35 to 40 inches (890-1,020 mm) of annual precipitation in areas where winter precipitation occurs in the form of rain, as in much of California; while in regions with heavy winter snows, St Johnswort may require little as 10 to 12 inches (250-300 mm) of annual precipitation. In areas receiving less than 10 inches (250 mm) annual precipitation St Johnswort invades drainageways where soil moisture is more abundant [78,154]. In northern Idaho, St Johnswort thrives in areas where mean annual precipitation ranges from 12 to 24 inches (300-610 mm) and soil moisture content is consistently reduced to 10 to 14% in the top 12 to 18 inches (30-46 cm) by early July. In several cases observed by Tisdale and others [177,178], St Johnswort plants remained green and apparently well supplied with moisture for periods of 2 to 4 weeks, when no available moisture was present above the 24-inch (61 cm) soil depth. Similarly, in California, soil in the upper 6 inches (15 cm) in St Johnswort-infested areas was near the wilting point from mid-spring throughout the summer. When the earliest St Johnswort flowers appear, late in April, the moisture in the upper soil layer has been exhausted and moisture is then drawn by St Johnswort almost entirely from depths of 10 to 35 inches (25-89 cm) [154].

Kudish [108] suggests that native *Hypericum* species in the Adirondack area require high water tables, but St Johnswort grows in well-drained sites and does not do well on poorly drained sites. This appears to be true in much of its introduced range [78,154]. Similarly, in an area on the Willamette Floodplain Research Natural Area in western Oregon, where mean annual precipitation is 40 inches (1,004 mm), St Johnswort cover has a moderately strong negative correlation (r=-0.91) with soil moisture index, which is related to microtopography. This area is characterized by a microtopography of mounds about 20 inches (50 cm) higher than the surrounding intermound matrix, and St Johnswort has higher cover on mounds (25.3%) than intermounds (0.9%), where soil moisture index is highest [169].

A review by Campbell and Delfosse [34] suggests that in Australia, St Johnswort is restricted by average annual rainfall of <20 inches (500 mm) at lower altitudes, and that the most vigorous infestations of St Johnswort occur in areas with an annual rainfall of >30 inches (760 mm). Drought may severely affect the appearance of a St Johnswort infestation, through reduced cover and flowering stem production, but will not reduce crown densities unless it is prolonged [22]. Regional differences in precipitation requirements may be due to different ecotypes of St Johnswort and/or to differences in soil types.

Soils:

St Johnswort grows in a wide variety of soil types, and soil parameters that may affect St Johnswort establishment and growth include moisture status, texture, fertility, depth, and pH. St Johnswort seems to prefer well-drained, coarse-textured soils [69,152,154,170]. In Washington, dense stands have become established on eroded, infertile areas of gravelly silt loam and on coarse sandy loam soils, as well as on fertile valley-bottom pasture land [78]. Soil fertility and depth may affect the growth habit and longevity of St Johnswort plants as observed in Australia (see Growth habit/stand type).

Soil pH may affect St Johnswort germination, establishment, and persistence, although experimental results are varied. Observations by Daubenmire (1947, as cited by [45]) and Sampson and Parker [154] suggest that St Johnswort is not common on calcareous soils, and seems to prefer soil with slightly acid to neutral pH. In California, Sampson and Parker [154] observed that while St Johnswort is not restricted to soils of either acid or alkaline reaction, unusually luxuriant growth and dense stands are more typically found on soils with pH 5 to 6.5, while very vigorous growth was not observed on strongly alkaline soils [154]. St Johnswort plants sprouted from lateral roots developed much more vigorously and flowered more profusely in acid medium (pH 6) than in alkaline medium (pH not given). Plants in alkaline medium did not form flowers, were smaller, and had light green foliage. Plants grown in extremely acid cultures (pH 3 to 4) died [154]. Borthwick [17] suggests that St Johnswort seed germination is inhibited by calcium ions. However, Campbell [32] found that neither added calcium nor calcium resident in the soil had a significant effect ($p<0.05$) on St Johnswort germination. Similarly, St Johnswort occurs on alkaline soils with pH ranging from 7.1 to 7.7 in an oak (*Quercus* spp.) savannah community type in on Pelee Island in the western Lake Erie archipelago [103]. St Johnswort also occurred only on plots (100% of them) that were previously plowed and had soils with high calcium and magnesium concentrations and higher pH (limed in past) than surrounding vegetation types in a Massachusetts study [133]. Additionally, of 5 woodland sites studied in southwestern England, St Johnswort seed was found only in the seed banks of the sites with basic soils, and not in acid soils (pH not given) [191]. Clark [41] suggests that St Johnswort infestation may be more strongly related to land use than to soil type.

Disturbance: As indicated in the discussion of general site characteristics, St Johnswort commonly occurs on disturbed sites such as agricultural fields, roadsides, railways, and "waste places," as well as forests disturbed by roads, logging, fire, and other factors that open the forest canopy. In California, St Johnswort invaded areas on denuded slopes and semi-exposed soils, where much of the surface soil horizon had been removed [154]. Much of the open forest and grassland areas in the Pacific Northwest and Intermountain area where St Johnswort infestations are most severe have (1) a history of heavy grazing [49,78,154,200], and (2) plant communities that are altered from their native condition and often dominated by nonnative species (see Successional Status). Where St Johnswort occurs in forested habitats, it seems to occur primarily on sites with some history of disturbance.

SUCCESSIONAL STATUS:
St Johnswort is an early successional species as evidenced by its frequent occurrence in disturbed areas. It may occur in the initial stages of plant development after a disturbance (e.g. [20,51,92,154,176,189]), and is also described as a secondary colonizer [75,166]. Its growth habit, persistence and longevity depend on a number of factors including soils, climate, shade, plant community, and site type (forest, grassland, agricultural field), and the presence and vigor of insect herbivores.

Soil fertility and depth may affect the growth habit and longevity of St Johnswort plants as observed in Australia (see Growth habit/stand type). St Johnswort persistence may be affected by elevation (see Site Characteristics), and it may be ephemeral under certain climatic conditions regardless of other site characteristics [22,41,45,154]. The median longevity of individual St Johnswort plants from 4 sites in Australia with varying climatic profiles was 3 to 6 years, with an overall range of 1 to 8 years. Very few St Johnswort crowns survived longer than 8 years. Death of individual crowns was attributed to drought, fire, defoliation by *Chrysolina* beetles, combinations of these, and senescence [22].

Several authors indicate that St Johnswort requires abundant light for best development. Evidence for this is provided by its occurrence in open grasslands and in open or disturbed forest sites, but not within undisturbed, dense forests, dense brush fields, or under the shade of trees in open forests [78,119,154]. Experimental evidence supports these observations. In a greenhouse test, St Johnswort plants subjected to approximately 50% of full daylight became distinctly pallid and droopy after 10 days, and nearly all of these plants died after 15 days [154]. Typically, where St Johnswort occurs in forested areas, it is often observed along roads and/or forest edges (e.g. [64,138,189]), in open areas within forests (e.g. [12,37,38]), or in early successional stages following fire, logging, or other disturbances (e.g. [39,138,162,178]). For example, on the H.J. Andrews Experimental Forest on the western slope of the Cascade Range in Oregon, St Johnswort was among those species that tended to increase as disturbance level and light level increased [138]. In the Lochsa River area in north-central Idaho, St Johnswort occurs on sites in the western redcedar-western hemlock zone that were previously forested until burned in 1919 and 1934, and have been dominated by seral shrubs for several decades [92,115,134].

Based on evidence of St Johnswort's presence at various stages of succession in some forest types (where data are available), it is unclear how long St Johnswort may persist in disturbed forest sites. In a grand fir/queencup beadlily (*Clintonia uniflora*) habitat type in the Selway-Bitterroot Wilderness in Idaho, St Johnswort occurred in a 15-year-old stand, but not in a 215-year-old stand [75]. Following the Sundance Burn in the western redcedar-western hemlock zone in northern Idaho, St Johnswort established in postfire year 4 and was last recorded on the site in postfire year 9 [164]. Stickney and Campbell [166] classify St Johnswort as an adventive, off-site colonizer based on data collected in forest communities at the Priest River Experimental Forest in Idaho that were clearcut in 1968 and broadcast burned in 1970. On 2 sites in Douglas-fir/ninebark (*Physocarpus malvaceus*) communities, St Johnswort established 12 to 15 years after disturbance. Percent cover of St Johnswort fluctuated after establishment and was recorded at 8% and 26% at the 2 sites 20 years after disturbance. In a western hemlock/queencup beadlily community, St Johnswort established at 1% cover 15 years after disturbance, persisted for 1 year and was absent after that [166].

These data suggest that St Johnswort does not persist in mature forest stands, and upholds the statement made in 1959 by Tisdale and others [178] that "serious spread of St Johnswort into 'well-stocked' forest stands has been observed only in open ponderosa pine." However, St Johnswort was found in several stages of succession in unmanaged, naturally regenerated, closed-canopy forests in the Douglas-fir/western hemlock zone of western Oregon, Washington, and northwestern California. Here St Johnswort was associated with young (35-79 yrs) age classes in the Oregon Coast Range, northern California, and southern Oregon; and was present in mature (80-95 yrs) and old growth (200-730 yrs) stands in the Oregon Coast Range, the Oregon Cascade Range, northern California, and southern Oregon [153]. Furthermore, over 80% of St Johnswort infestations in Australia occur in native eucalyptus forests (Shepherd as cited by [22,24]). Evidence presented by Buckley and others [24] indicates that St Johnswort plants growing in shaded sites grow more slowly and produce less fruit but live longer. Additionally, although St Johnswort may not be present in aboveground forest vegetation, viable St Johnswort seed sometimes occurs in forest soils (e.g. [76,114,117]). Consequently, St Johnswort plants may establish and spread following disturbance (see Seed banking).

St Johnswort populations in shaded conditions may be evolving in response to current conditions experienced in their recipient community (sensu [121]), or possibly in response to selection pressures from introduced herbivores. Where *Chrysolina*
beetles are well established for biological control of St Johnswort in Canada, St Johnswort appears to do better in shaded conditions, as the beetles are not shade tolerant. At Fruitvale, British Columbia, St Johnswort and beetle densities in open sites were compared to those in sites receiving about one-half day of sunlight and with places receiving less than one-half day of sunlight. St Johnswort did not flower in the partial shade, and neither St Johnswort nor beetles occurred in densely shaded plots. St Johnswort had the greatest stem density in the greatest shade and the least in open, sunny sites. The more shaded areas also had the fewest *Chrysolina hyperici*; thus, the shade seems to provide a partial sanctuary for St Johnswort [84]. Conversely, in open eucalyptus woodland and an adjacent clearing in Australia, *C. quadrigemina* occurred in similar densities in both open and timbered areas. This is unusual since the beetle normally avoids shaded situations and inflicts little damage on St Johnswort plants growing in such conditions [20].

St Johnswort is also a common component of early to mid-successional vegetation on abandoned agricultural land in many areas of North America (e.g. [13,57,60,61,133,154]). On Montague Plain in central Massachusetts, St Johnswort occurred only on plots (100% of them) that were plowed 30-50 years previous [133]. According to Beckwith [13], St Johnswort may be common in the mixed herbaceous perennial stage of old-field succession in Michigan, which usually predominates 11 to 15 years after abandonment from grain crops and 16 to 20 years after abandonment from cultivated and hay fields. Some authors indicate that as old fields succeed to woodlands, St Johnswort goes away as trees and shrubs take over (e.g. Wilson 1943, as cited by [78]). In a study of old-field succession in southeastern Connecticut, St Johnswort was present in the early stages of succession, but was absent from the community 20 to 30 years later, as plant communities succeeded either to young hardwood forest dominated by black cherry (*Prunus serotina*) and red maple, or vine communities dominated by Oriental bittersweet (*Celastrus orbiculata*) [60]. Reader [148] presents evidence that suggests that granivory may remove larger seeds of later successional species and leave smaller seeds, such as those of St Johnswort, thus retarding old field succession.

In the parts of North America where St Johnswort is most invasive and considered most problematic, St Johnswort typically established in grasslands that had been severely overgrazed in the early 1900s. At the time that St Johnswort established and spread, these grasslands were no longer dominated by native species, but were typically dominated by nonnative annual grasses and other undesirable plants. Grasslands throughout the interior Columbia Basin, where native perennial grasses have been replaced by nonnative annual grasses such as cheatgrass, are susceptible to invasion by nonnative invasive perennial forb species such as knapweeds (*Centaurea* spp.) and St Johnswort [26,79,94,95,177,184]. According to Tisdale and others [178], St Johnswort invasion into grasslands in northern Idaho was facilitated by the "depleted condition" of these grasslands, on which the perennial climax dominants had been largely replaced by annual grasses (mainly brome species) and annual forbs. Rapid development and deep penetration of roots of young St Johnswort plants aids in withstanding the critical summer drought period in these areas, and St Johnswort's deep and extensive root system may allow it to outcompete the annuals for water and nutrients [178]. Similarly, St Johnswort commonly invaded annual grassland sites in northern California that were once dominated by perennial grasses [93]. According to Sampson and Parker [154], St Johnswort shades out the shorter grasses and depletes moisture in the upper soil layers to the point of excluding other vegetation. California oatgrass (*Danthonia californica*) is among the last of the grasses to be replaced by St Johnswort, while winter annuals tend to persist as St Johnswort increases in density. A late successional St Johnswort invasion is described as a dense stand of St Johnswort with an understory of winter annuals [154]. No definite data as to the longevity of St Johnswort in grasslands exist; however, Harris [78] cites observations of 40- to 50-year-old St Johnswort infestations (as of 1951) on California rangeland.

St Johnswort populations were severely impacted, and successional trajectories further altered, in some areas following the North American introduction of biological control agents for St Johnswort [31,160,177]. These reductions were followed by increases of different plants in different areas. In the Interior Columbia Basin, successful biological control of St Johnswort was followed by a return to annual grass dominance [26,177]. Many pastures in Oregon that were once infested with St Johnswort became infested with tansy ragwort (*Senecio jacobaea*) after St Johnswort was reduced by biological agents [43]. In northern Idaho, the overall abundance of St Johnswort fluctuates around 3% of that present in 1948. As yield and frequency decreased in St Johnswort, annual forbs and grasses increased, with annual bromes being most common, along with foxtail fescue (*Vulpia myuros*), and the relatively new arrival of medusahead. Perennial forbs and grasses increased to a lesser extent. Natural recovery of bluebunch wheatgrass in these areas is thought to be inhibited by inadequate seed source, competition from annual grasses, and continuing heavy grazing on many sites [177]. Campbell and McCaffrey [31] found that where St Johnswort is suppressed by biocontrol insects in northern Idaho, replacement vegetation is dominated by annual grasses and weedy forbs such as knapweeds and field bindweed (*Convolvulus arvensis*). Spotted knapweed (*Centaurea maculosa*) has largely replaced St Johnswort throughout the northernmost areas of Idaho. At 1 site yellow starthistle (*C. solstitialis*) succeeded medusahead, which invaded after St Johnswort was initially reduced by biocontrol agents (personal communication by M. Hironaka as cited in [31]). On annual grasslands in northern California, St Johnswort was reduced to less than 1% of its former occurrence 10 years after establishment of biocontrol insects. This reduction was accompanied by a concurrent increase in perennial grasses (mainly California oatgrass) in Humboldt County, and an increase in winter annual grasses, legumes, and other forbs in other areas. No major increases of other invasive species were reported at the time (1959), although yellow starthistle and medusahead were both present on several sites [93]. It is unclear how biological control insects of St Johnswort may affect succession in other areas where the insects have less total impact on St Johnswort populations.

SEASONAL DEVELOPMENT:
St Johnswort seeds germinate in autumn, winter, or spring. Erect woody stems develop in late winter to spring. Flowering and pollen production begin late spring to early summer and continue well into summer, although 1st-year plants do not flower. By mid-summer most petals have withered; seed capsules are moist, green, and sticky; and seeds are green. In early autumn few petals remain, and capsules dry and become less sticky. By late autumn all petals have gone, flowering stems are dry, and capsules contain ripe seeds. Dry flowering stems remain standing for several months, sometimes years [34,45,139,178].

Fall and winter rains initiate procumbent growth in St Johnswort, with prostrate, nonflowering stems up to 12 inches (30 cm) long [34,45,121]. Foliage may be thick on these stems and form a thick mat that smothers other vegetation [34,139]. St Johnswort overwinters in this form, and by seed [45]. Procumbent stems die in late spring [34].

The general phenological pattern observed on a study area in northern Idaho from 1950 through 1956 was as follows [178]:

Drainage	Elevation (feet)	Start of upright shoots	Early bloom	Late bloom	Early fruit	Ripe seed
Clearwater	1,200	1st week April	1st week June	2nd week July	4th week July	2nd week September
Salmon	1,800	2nd week April	2nd week June	2nd-3rd week July	4th week July	2nd week September
Palouse	3,500	4th week April	3rd week June	4th week July	1st week August	2nd-3rd week September

In northern Idaho, St Johnswort remained green longer than most of the associated vegetation including native perennials. Most seed was ripe by mid-September, and seed dissemination occurred through October and November. At most sites, and in 4 of the 7 years during the observation period, St Johnswort produced fall procumbent basal growth, varying from about 1 to 5 inches (2-13 cm) long. Some winter damage to fall growth was noted, especially on sites with erratic snow cover [178]. Walker [189] provides detailed observations of timing of flowering and seed production at a site in Oregon.

Flowering dates in other parts of North America are given as follows:

Geographic area	Flowering dates	Reference
CA	June to September	[136]
KS	June to October	[9]
southeastern MI	June 19 to August 16	[57]
NV	June to September	[100]
TX	June to September	[52]
WV	June-September	[168]
Adirondack area	July 11 through summer	[108]
Blue Ridge	June to August	[199]
Carolinas	June to September	[145]
Great Plains	June to August	[69]
north Atlantic coast	June to September	[54]
northeastern U.S.	June to September	[67]
NS	July 10-August	[152]
eastern Canada	late June to August	[45]

FIRE ECOLOGY

SPECIES: Hypericum perforatum

FIRE ECOLOGY OR ADAPTATIONS:

Fire adaptations:

Mature St Johnswort plants have deep, extensive perennial root systems, and reproduce vegetatively from lateral roots and root crowns. Vegetative propagation in St Johnswort seems to be stimulated by grazing, fire, and defoliation [41,178] (see Asexual regeneration). This adaptation allows St Johnswort to survive even severe fire, depending on site conditions. A protective tissue of suberized cells called polyderm has been described on St Johnswort roots (Esau 1960, as cited by [45]). It is unclear whether this tissue might provide protection from heat.

St Johnswort also establishes from seed, and St Johnswort seed is commonly found in soil seed banks. Estimates of 6 to 30 years or more have been suggested for longevity of viable St Johnswort seed in soil seed banks (see Seed banking). Additionally, heat seems to stimulate germination in St Johnswort seed, and researchers have observed flushes of St Johnswort seedlings following fire [20,154,189]. See Discussion and Qualification of Fire Effect for more details.

Fire regimes:

St Johnswort occurs in a wide variety of ecosystems in North America which represent a wide range of historic fire regimes. In many areas where St Johnswort occurs, historic fire regimes have been dramatically altered due to fire exclusion and to massive disturbances associated with human settlement. The historic fire regimes of native communities in which St Johnswort sometimes occurs range from low frequency, high-severity stand replacing fires in wet forest types; to high frequency, high-severity fires in prairie grasslands; to high frequency, low-severity fires in open ponderosa pine forests. St Johnswort did not occur in these communities at the time in which historic fire regimes were functioning, but has established since fire exclusion and habitat alteration began. It is unclear how historic fire regimes might affect St Johnswort populations.

St Johnswort also occurs in areas where annual grasses such as cheatgrass are dominant. Fire regime change due to invasion of annual grasses is well documented [23,47] (see cheatgrass in FEIS). Cheatgrass expansion has dramatically changed fire regimes and plant communities over vast areas of western rangelands by changing the fuel properties of invaded communities (sensu [23]) and thus creating an environment where fires are easily ignited, spread rapidly, cover large areas, and occur frequently [204]. Short fire return intervals in cheatgrass-dominated communities (<10 years [141,194]) may favor St Johnswort, with its large root system, ability to sprout after injury, and seed germination stimulated by heat. More research and field observations are needed to understand how St Johnswort responds to the current fire ecology of these areas.

It is also unclear how the presence of St Johnswort might affect fire regimes in invaded communities. In general, in ecosystems where St Johnswort replaces plants similar to itself (in terms of fuel characteristics), St Johnswort may alter fire intensity or slightly modify an existing fire regime. However, if St Johnswort is qualitatively unique to the invaded ecosystem, it has the potential to completely alter the fire regime (sensu [23,47]). Two authors suggest that presence of dry senescent stems of St Johnswort create a fire hazard in forest areas in California [154] and Australia [139]. It is unclear whether these assertions are based on conjecture or on observations made by the authors. No examples of historic fire regimes altered by St Johnswort invasion are described in the available literature.

The following list provides fire return intervals for plant communities and ecosystems where St Johnswort may be important. If you are interested in plant communities or ecosystems that are not listed, see the complete FEIS fire regime table.

Community or Ecosystem	Dominant Species	Fire Return Interval Range (years)
silver fir-Douglas-fir	*Abies amabilis-Pseudotsuga menziesii* var. *menziesii*	> 200
grand fir	*Abies grandis*	35-200 [3]
maple-beech-birch	*Acer-Fagus-Betula*	> 1,000
silver maple-American elm	*Acer saccharinum-Ulmus americana*	< 35 to 200
sugar maple	*Acer saccharum*	> 1,000
sugar maple-basswood	*Acer saccharum-Tilia americana*	> 1,000 [188]
California chaparral	*Adenostoma* and/or *Arctostaphylos* spp.	< 35 to < 100 [140]

bluestem prairie	*Andropogon gerardii* var. *gerardii-Schizachyrium scoparium*	< 10 [106,140]
silver sagebrush steppe	*Artemisia cana*	5-45 [88,144,201]
sagebrush steppe	*Artemisia tridentata/Pseudoroegneria spicata*	20-70 [140]
basin big sagebrush	*Artemisia tridentata* var. *tridentata*	12-43 [155]
mountain big sagebrush	*Artemisia tridentata* var. *vaseyana*	15-40 [5,27,126]
Wyoming big sagebrush	*Artemisia tridentata* var. *wyomingensis*	10-70 (40**) [186,204]
coastal sagebrush	*Artemisia californica*	< 35 to < 100 [140]
plains grasslands	*Bouteloua* spp.	< 35 [140,201]
cheatgrass	*Bromus tectorum*	< 10 [141,194]
California montane chaparral	*Ceanothus* and/or *Arctostaphylos* spp.	50-100 [140]
sugarberry-America elm-green ash	*Celtis laevigata-Ulmus americana-Fraxinus pennsylvanica*	< 35 to 200 [188]
curlleaf mountain-mahogany*	*Cercocarpus ledifolius*	13-1,000 [7,156]
northern cordgrass prairie	*Distichlis spicata-Spartina* spp.	1-3 [140]
beech-sugar maple	*Fagus* spp.-*Acer saccharum*	> 1,000 [188]
California steppe	*Festuca-Danthonia* spp.	< 35 [140,167]
black ash	*Fraxinus nigra*	< 35 to 200 [188]
juniper-oak savanna	*Juniperus ashei-Quercus virginiana*	< 35
western juniper	*Juniperus occidentalis*	20-70
Rocky Mountain juniper	*Juniperus scopulorum*	< 35 [140]
cedar glades	*Juniperus virginiana*	3-22 [74,140]
western larch	*Larix occidentalis*	25-350 [4,11,50]
wheatgrass plains grasslands	*Pascopyrum smithii*	< 5-47+ [140,144,201]
Great Lakes spruce-fir	*Picea-Abies* spp.	35 to > 200 [53]
pine-cypress forest	*Pinus-Cupressus* spp.	< 35 to 200 [3]
pinyon-juniper	*Pinus-Juniperus* spp.	< 35 [140]
Rocky Mountain lodgepole pine*	*Pinus contorta* var. *latifolia*	25-340 [10,11,172]
Sierra lodgepole pine*	*Pinus contorta* var. *murrayana*	35-200
western white pine*	*Pinus monticola*	50-200
Pacific ponderosa pine*	*Pinus ponderosa* var. *ponderosa*	1-47 [3]
interior ponderosa pine*	*Pinus ponderosa* var. *scopulorum*	2-30 [3,8,112]
red pine (Great Lakes region)	*Pinus resinosa*	10-200 (10**) [53,65]
red-white-jack pine*	*Pinus resinosa-P. strobus-P. banksiana*	10-300 [53,87]
eastern white pine	*Pinus strobus*	35-200

eastern white pine-eastern hemlock	*Pinus strobus-Tsuga canadensis*	35-200
eastern white pine-northern red oak-red maple	*Pinus strobus-Quercus rubra-Acer rubrum*	35-200
Virginia pine	*Pinus virginiana*	10 to < 35
Virginia pine-oak	*Pinus virginiana-Quercus* spp.	10 to < 35
sycamore-sweetgum-American elm	*Platanus occidentalis-Liquidambar styraciflua-Ulmus americana*	< 35 to 200 [188]
eastern cottonwood	*Populus deltoides*	< 35 to 200 [140]
aspen-birch	*Populus tremuloides-Betula papyrifera*	35-200 [53,188]
quaking aspen (west of the Great Plains)	*Populus tremuloides*	7-120 [3,73,125]
black cherry-sugar maple	*Prunus serotina-Acer saccharum*	> 1,000 [188]
mountain grasslands	*Pseudoroegneria spicata*	3-40 (10**) [2,3]
Rocky Mountain Douglas-fir*	*Pseudotsuga menziesii* var. *glauca*	25-100 [3,5,6]
coastal Douglas-fir*	*Pseudotsuga menziesii* var. *menziesii*	40-240 [3,132,151]
California mixed evergreen	*Pseudotsuga menziesii* var. *menziesii-Lithocarpus densiflorus-Arbutus menziesii*	< 35
California oakwoods	*Quercus* spp.	< 35 [3]
oak-hickory	*Quercus-Carya* spp.	< 35
northeastern oak-pine	*Quercus-Pinus* spp.	10 to < 35 [188]
coast live oak	*Quercus agrifolia*	2-75 [70]
white oak-black oak-northern red oak	*Quercus alba-Q. velutina-Q. rubra*	< 35 [188]
canyon live oak	*Quercus chrysolepis*	<35 to 200
blue oak-foothills pine	*Quercus douglasii-P. sabiniana*	<35 [3]
northern pin oak	*Quercus ellipsoidalis*	< 35 [188]
Oregon white oak	*Quercus garryana*	< 35 [3]
California black oak	*Quercus kelloggii*	5-30 [140]
oak savanna	*Quercus macrocarpa/Andropogon gerardii-Schizachyrium scoparium*	2-14 [140,188]
northern red oak	*Quercus rubra*	10 to < 35
post oak-blackjack oak	*Quercus stellata-Q. marilandica*	< 10
black oak	*Quercus velutina*	< 35
live oak	*Quercus virginiana*	10 to< 100 [188]
interior live oak	*Quercus wislizenii*	< 35 [3]
little bluestem-grama prairie	*Schizachyrium scoparium-Bouteloua* spp.	< 35 [140]
western redcedar-western hemlock	*Thuja plicata-Tsuga heterophylla*	> 200
western hemlock-Sitka spruce	*Tsuga heterophylla-Picea sitchensis*	> 200
mountain hemlock*	*Tsuga mertensiana*	35 to > 200 [3]
elm-ash-cottonwood	*Ulmus-Fraxinus-Populus* spp.	< 35 to 200 [53,188]

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

POSTFIRE REGENERATION STRATEGY [165]:
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: Hypericum perforatum

IMMEDIATE FIRE EFFECT ON PLANT:
Little information is available regarding the immediate effects of fire on St Johnswort stems, roots, and seeds. Fire is likely to top-kill St Johnswort; however, fire may or may not damage St Johnswort root crowns and lateral roots. One author reports that St Johnswort lateral roots occur 0.5 to 3 inches (1-8 cm) below the soil surface [41], a depth at which they may be damaged by severe fire. Evidence presented by Sampson and Parker [154] and field observations by other researchers [20,189] suggest that fire may stimulate sprouting from undamaged St Johnswort roots and root crowns, and germination in St Johnswort seeds. According to observations presented by Agee [1], even high-severity fire may stimulate sprouting and/or seed germination in St Johnswort.

DISCUSSION AND QUALIFICATION OF FIRE EFFECT:
Field observations [20,154,189] and laboratory tests [154] suggest that fire stimulates germination in St Johnswort seed, although it is unclear how fire severity and season of burning may affect germination response in St Johnswort.

In fall 1996, more than 1,000 acres (400 ha) of land planted to hard fescue (*Festuca trachyphylla*), tall wheatgrass (*Thinopyrum ponticum*), and alfalfa (*Medicago sativa*) were burned under prescription at the Kilby Ranch in Oregon. Before the burn, isolated patches of St Johnswort occurred around the perimeter of the ranch, with the largest patches south of the burn area. Within 7 months of the fire, immature St Johnswort plants (presumably seedlings, although this is not clearly stated) established across the burn area. The following season (1998), St Johnswort plants had matured and the St Johnswort infestation was very dense. By the 3rd postfire year (1999), St Johnswort had spread beyond the boundary of the burn area. The author suggests that an extensive St Johnswort seed bank was present and stimulated to germinate by the fire [189].

Similarly, a rangeland site was burned twice under prescription in California in October of 1926 and 1927 in an effort to control St Johnswort. The fire completely consumed St Johnswort crowns, and apparently stimulated germination in St Johnswort seed. The authors describe large numbers of St Johnswort seedlings where the fire had been "very hot." Timing of seedling emergence relative to time of burning is not given, nor do the authors indicate how it was determined that St Johnswort plants were seedlings and not root sprouts. The authors do indicate that a temperature of 260 °F (127 °C) was recorded at 0.25 inch (0.6 cm) below the soil surface in selected localities during the field burning operation, but they do not describe how this was measured, or any other temperatures recorded during the burn. Based on their observations, the authors conducted laboratory experiments to test the effects of various heat treatments on St Johnswort seed. An oven was used to expose St Johnswort seeds to 212 °F (100 °C) for 5, 15, 30, and 60 minutes; or to 260 °F (127 °C) for periods of 1 to 5 minutes. Seeds were then placed in sterilized sand and germinated in the greenhouse. The unheated control seed lots had the lowest germination rate at 44%, while seed lots exposed to 212 °F (100 °C) for 5, 15, 30, and 60 minutes had germination rates of 52%, 63%, 81%, and 75%, respectively. The germination rates of seed exposed to 260 °F (127 °C) were not given, although the authors state, "even at this temperature the seed gave a distinctly higher percentage of germination than did the untreated seeds" [154].

It is unclear whether germination of St Johnswort seed after fire is a function of heat stimulation of germination or of reduction in plant cover that allows for seedling emergence. For example, Greiling and Kichanan [71] found that St Johnswort seedling emergence was 100 times higher ($p<0.01$) when plant neighbors (little bluestem and old field species) were removed.

According to Agee [1], severe burning associated with log corridors in disturbed Oregon white oak woodlands provides favorable sites for many nonnative species such as St Johnswort, common velvetgrass (*Holcus lanatus*), and tansy ragwort. It is unclear whether the author refers to seedlings or to sprouts from established roots or root crowns, and what this observation is based on.

PLANT RESPONSE TO FIRE:
It is generally purported that fire encourages establishment, vegetative spread, and increased density of St Johnswort patches [34,41] by stimulating germination of St Johnswort seed (see Discussion and Qualification of Fire Effect) and sprouting in surviving St Johnswort roots and root crowns [20,154,178]. Several references indicate that St Johnswort often occurs in previously burned areas, especially forests (e.g. [34,37,38,39,41,58,113,169,178]).

Accounts in the literature of St Johnswort's response to fire are varied, from no response; to immediate increases in cover and/or density; to immediate decreases in cover and/or density, followed by increases several postfire years later. Because most information available in the literature on St Johnswort's response to fire comes from studies in which the response of St Johnswort to fire was not the primary objective of the study, and because all variables and details of fires are not consistently reported, it is unclear why results differ among reports.

DISCUSSION AND QUALIFICATION OF PLANT RESPONSE:
Variation in St Johnswort response to fire may be affected by plant community type, fire size, fire severity and/or season of burning.

A study from New South Wales, Australia, suggests that fire severity, as influenced by plant community type and associated fuel loads, may affect St Johnswort's response to fire [20]. During the course of monitoring populations of biological control insects in a native forest in southeastern New South Wales, a monitoring site was burned under prescription in an effort to reduce risk of major wildfires. Briese [20] examined the effects of these fuel reduction burns on St Johnswort populations and populations of associated biological control insects at this site.

The study site included areas with 2 distinct plant communities: an area of open woodland dominated by eucalyptus species (*Eucalyptus pauciflora* and *E. stellulata*) and an area in an adjacent clearing. Before burning, ground cover consisted of perennial grasses and various forbs including St Johnswort. In the open area total ground cover was 50% to 70%, with 12% to 36% St Johnswort. In the timbered area, total ground cover was 22% to 44% total with 12% to 24% St Johnswort. The site was burned in spring (September) 1982. Details of the fire were not given; however, fire intensity (severity) was estimated from the percentage of ground cover consumed, mortality of marked St Johnswort plants, and height of crown scorch in the timbered area. In the open area, ground cover was reduced 59% ± 11%, with 9% mortality of St Johnswort crowns. St Johnswort cover returned to prefire levels (12% to 36%) rapidly in the open area, with a slight increase in crown density within months of the fire. In the timbered area, ground cover was reduced 100%, with 64% St Johnswort crown mortality. St Johnswort recovered more slowly in the timbered area than in the open area, although it recovered more rapidly than associated vegetation, mainly by growth from surviving roots. By summer (January) 1984, St Johnswort had reached 65% cover in the timbered area, mainly due to enhanced growth of individual plants rather than an increase in crown density. A similar, but less extreme increase (to about 45% cover) of St Johnswort was seen in the open plots. The net result was a very large increase in the production of St Johnswort flowering stems and seed in both areas in the summer of 1983/1984 [20].

Germination of St Johnswort seeds in the 1st postfire season was higher than average, but contributed little to plant recovery. Postfire growth of St Johnswort was mainly from surviving roots, whereas associated grasses and herbs reestablished from seeds that did not germinate until the following autumn. A regression of vegetative regeneration against the proportion of original crown surviving the fire suggests that fire can stimulate regrowth in surviving rootstocks. When damage is light, as in the open plots, this can lead to regeneration that is greater than the replacement rate, resulting in an increase in the proportion of crowns originating from roots after the fire (from 78.3% ± 2.8% to 91.6% ± 2.1% in the open area and from 82.7% ± 4.8% to 93.8% ±
2.4% in the timbered area, $p<0.05$ in both cases). In the severely burned timbered plots, regeneration did not equal replacement, though growth of individual plants was greatly enhanced. The response of St Johnswort and of introduced biocontrol insects to increased soil fertility following fire is important to postfire population dynamics of both (see Fire interactions with other control methods) [20].

Results presented by Hooker and Tisdale [92] following prescribed burning on a seral brush community in the Lochsa River area in northern Idaho suggest a somewhat different relationship of St Johnswort recovery relative to fire severity. The authors state that St Johnswort "increased following low intensity burning but did not benefit when the treatment was more intense." However, plant recovery was only measured for 1 season following burning, and the data upon which this conclusion was based were not provided. Surface soil temperatures were measured in this study using pyrometers, and sites with highest recorded temperatures supported dense stand of old brush (various shrubs) and bracken fern. Bracken fern recovered rapidly following fire and grew in dense stands, possibly explaining why St Johnswort did not recover as well on high severity sites [92].

Season of burning may also affect St Johnswort response. A 2nd prescribed fire was conducted in the New South Wales study area (described above) in fall (March) 1986. In the open area, ground cover was reduced 96% ± 2%, while ground cover was reduced 85% ±
9% in the timbered area by the fall burn. There was massive germination of herbs and grasses, including St Johnswort, following the fall burn. Because St Johnswort seedlings are poor competitors, the native grass and forb component remained dominant in both areas in 1987, despite some recovery of mature St Johnswort plants [20].

Other fire studies where St Johnswort occurred in the plant community but was not the focus of the study provide no clear picture of St Johnswort's response to fire. Results from studies in Oregon, Washington, and Idaho are presented to demonstrate the variability of this response. A native wetland prairie site in Willamette Valley, Oregon, dominated by tufted hairgrass and invaded by several woody species, was treated to remove woody species by burning, hand-removal, or mowing. St Johnswort was present before treatments were imposed. Where plots were burned or woody plants removed by hand, St Johnswort cover was also reduced. The authors speculate that this reduction may have been due to increased abundance of insect herbivores with increased light [40]. A moderate-severity fire in a snowberry-rose association in northeastern Oregon had little effect on St Johnswort cover. Prefire cover of St Johnswort averaged 1% in a stock exclosure and 10% in a game exclosure. No St Johnswort was found 1 year after fire, and St Johnswort cover was 3% in the stock exclosure and 9% in the game exclosure 5 years after fire [96]. Thickets of scotchbroom in prairies and oak woodlands in Ft. Lewis, Washington, were burned under prescription in fall (September) 1994 to try to reduce frequency and density of scotchbroom. Average prefire cover of St Johnswort was 1.1%, and postfire cover, recorded in May 1995, was 1.9%. These results indicate no significant ($p<0.05$) change in St Johnswort cover; however, the duration of the study is insufficient to be conclusive. Additionally, no data are given for St Johnswort response to spring burning in the same study (some fire details are given) [180]. Brush covered slopes in northern Idaho were burned in May 1975, and seeded with several nonnative herbaceous species in May 1975 in an effort to improve winter/spring forage for elk. Plant frequency and green weight production were measured for 4 growing seasons following burning. St Johnswort "occurred on all 3 study areas and did not show any obvious changes following any treatment" (some fire details are given) [115].

FIRE MANAGEMENT CONSIDERATIONS:

Fire as a control agent:

While experimental evidence is inconclusive regarding St Johnswort's response to fire, much of the available literature suggests that fire increases frequency and density of St Johnswort [20,34,41,154,178]. Therefore, burning is not indicated as a potentially effective method for controlling St Johnswort. Other evidence suggests that, in some cases, burning may provide effective control for St Johnswort. Very little literature examines the effects of prescribed burning intended to control St Johnswort.

According to Sampson and Parker [154], some stockmen contend that burning infestations of St Johnswort when the tops are dry in autumn will kill the present cover and destroy the accumulated seed. By burning 2 or 3 years in succession it was suggested that grass may invade the area and crowd out any remaining St Johnswort plants. To test these suggestions, 300 acres (120 ha) near Blocksburg, California was burned "closely" in October of 1926 and 1927. The fire completely consumed St Johnswort tops, and "carried" to all isolated patches, leaving no tops unburned. Density of St Johnswort was measured before the 1st burn and after the 2nd burn in "representative" areas. However, these data are not reported, nor do the authors indicate how long after burning density measurements were taken. The authors summarize results by stating "instead of the weed cover being killed or subsequently thinned out by invading grasses, the stand of St Johnswort was denser and seemingly more vigorous than before." They further suggest that not only does fire stimulate germination of St Johnswort seed, but that repeated burning may deplete the soil of organic material and thus favor St Johnswort and other undesirable plants [154]. Similarly, at Dye Creek and Vina Plains Preserves in California, St Johnswort is said to be encouraged by burning, and the preserves' manager recommends against using prescribed fire in St Johnswort-infested areas [149].

Conversely, preserve managers for The Nature Conservancy in Michigan and Ohio indicate that fire suppression encourages invasion of St Johnswort, while burning and restoration treatments discourage invasion of St Johnswort. At Kitty Todd, Ohio, where St Johnswort is found in areas that were previously farmed and grazed and around old homesites, burning "seems to be somewhat effective" as a control method for St Johnswort. Unfortunately, further details on how and when burning was conducted are not available [149].

According to Jack McGowan-Stinski, Fire Manager for Michigan sites of The Nature Conservancy, St Johnswort has been reduced or eradicated with both prescribed fire and spot-burning (using propane torches), with and without additional control methods. Control, using either prescribed or spot-burning, is most successful in dry sand prairies and oak barrens, possibly due to nutrient-poor soil conditions. Prescribed burning on sites where there is a diversity of native prairie grasses (little bluestem, big bluestem, prairie dropseed (*Sporobolus heterolepis*), and sideoats grama (*Bouteloua curtipendula*)) and native forbs eliminates St Johnswort when burning is conducted during the growing season or early fall (June, July, August), and repeated for 2 to 3 consecutive years. Native plants on these sites are adapted to fires during this season and out-compete St Johnswort in the postfire environment. In areas with dense St Johnswort populations, repeated spot-burning has successfully reduced or eliminated St Johnswort. This is also likely due to native perennial prairie plants' tolerance of repeated burning (in the same year) in late summer or early fall. Prescribed or spot burning followed by hand removal of St Johnswort sprouts and seedlings by volunteers throughout the season is also successful. The advantages of burning followed by hand removal include fewer restrictions by weather, staff time, and equipment, and lower associated costs [123].

Fire interactions with other control methods: Fire managers may need to include the existence of biological control agents in their decision making process and fire management plans. Fire may adversely affect populations of biological control agents and thus lead to increases in host plant populations. In the Awatere Valley of New Zealand, the only reported resurgence of St Johnswort following successful control by *Chrysolina hyperici* occurred following a fire (Syrett 1989, as cited by [20]). Intensity, frequency, and season, plus scale of individual fires are important for both the host weed and the biological control agent. The final outcome depends on how a particular weed or biological control agent responds to these components of the fire regime [20].

One study in Australia examines effects of fuel reduction burns on biological control of St Johnswort. Details of the study site and St Johnswort response to burning are given above (see Discussion and Qualification of Plant Response). St Johnswort on this site supported populations of *C. quadrigemina*, a chrysomelid beetle introduced to Australia for biological control of St Johnswort [20].

The immediate effect of the spring 1982 prescribed fire on *C. quadrigemina* was the virtual disappearance of the insect during 1983, with only a few eggs observed during that period. In autumn 1984, massive egg-laying and subsequent larval defoliation of rosettes were observed, most likely due to re-invasion by adult beetles from neighboring unburned plots. Large-scale destruction of St Johnswort by beetles was repeated in 1985. This resulted in a substantial decrease in St Johnswort ground cover, crown density, and production of flowering stems, and an increase in dominance of the grass and forb component in both open and timbered areas. Briese [20] suggests that a short term postfire increase in soil nutrients ("the fertilizer effect") may have contributed indirectly to the impact of the biological control agent on St Johnswort. Nutrient analyses of St Johnswort plants collected the season following the fire showed a 25% increase ($p<0.05$) in nitrogen levels in plants from burned areas relative to plant from adjacent unburned areas. Burned plants were also larger than average, which may have been particularly attractive to beetles and/or favor survival and development of hatching larvae, thus triggering a population build-up of the biological control agents [20].

Following the fall 1986 fire, St Johnswort populations and associated grasses and forbs responded much differently, with massive seed germination of several species, including St Johnswort. Most St Johnswort seedlings did not survive and persist, and associated grasses and forbs dominated the postfire environment. Large populations of *C. quadrigemina* were not observed on the site until 1990 [20].

Frequency of fire is a key factor for effects on biocontrol agents, and the cycle of their population build-up needs to be understood and respected to enable them to have the desired impact on the target weed. The frequency of prescribed burning may need adjusting according to the reproductive capacity and life history of the control agent. Reproductive strategy and mobility of control agents are important factors to consider. If one considers both fire management and biological control as long-term protection strategies, it is necessary to look at the interaction of weed biology, control agent biology, fire regime, and whether they can be manipulated to help realize the potential of the control agent, or at least to not hinder it [20].

Postfire colonization/spread potential: Several sources suggest that St Johnswort has high potential for postfire colonization in some areas. Several references indicate that St Johnswort often occurs in previously burned areas, especially forests (e.g. [34,39,41,113,128,169,178]). The source (seeds vs. sprouts) of St Johnswort establishment in these references is unclear. St Johnswort may occur in the initial postfire community by establishing from root crowns, roots, or seeds in the soil seed bank, or it may occur in burned areas as a secondary colonizer, establishing from off-site sources some years after fire.

Where St Johnswort occurs as mature plants, it is likely to occur in the initial postfire community (e.g. [20,40,115,180]), although it may or may not persist (See Successional Status). Several studies in which the soil seed bank was sampled and germinated indicate the presence of St Johnswort seed in areas where mature plants are rare, do not occur, or occur only at some distance from the sampled sites [76,111,114,117,197]. Harris and Gill [81] suggest that when a pine plantation (or forest) reaches stand closure, St Johnswort may disappear from aboveground vegetation, but remain (as seed) in the soil seed bank (see Seed banking for details). When fire occurs in such sites, St Johnswort may establish from seed as part of the initial postfire community. Rapid postfire infestation of St Johnswort following prescribed burning on an Oregon range site suggests that an extensive seed bank was present on the site before the fire [189] (see Discussion and Qualification of Fire Effect). Evidence of St Johnswort establishment following disturbances from timber harvest or thinning (e.g. [51,176]) further support the possibility of St Johnswort establishment after a fire that reduces or removes canopy cover and/or disturbs the soil.

Although there is no clear evidence in the literature, managers should be aware that St Johnswort may also establish as an initial off-site colonizer in areas where St Johnswort populations are in the vicinity of a burn site and seed may be transported by wild or domestic animals, or by vehicles.

St Johnswort may also establish as a secondary off-site colonizer that establishes after postfire year 1 [164]. Evidence to support this is provided from several forested habitats in Idaho [75,164,166], where St Johnswort established several years after fire and did not persist as canopies established. St Johnswort may, however, persist in closed-canopy Douglas-fir forests (e.g. [153]), as well as in more open-canopied forests such as some eucalyptus [22,24] and ponderosa pine forests [178] (see Successional Status).

Several authors suggest that spread of St Johnswort is also encouraged by fire in some areas and under some conditions [20,149,154,189].

According to Campbell and Delfosse (1984) when stands of St Johnswort are burned, density of the stand increases. Thus, control of rangeland fires may be important to the control of St Johnswort [45].

Preventing postfire establishment and spread: The USDA Forest Service's "Guide to Noxious Weed Prevention Practices" [181] provides several fire management considerations for weed prevention in general that apply to St Johnswort.

Preventing invasive plants from establishing in weed-free burned areas is the most effective and least costly control method. This can be accomplished through careful monitoring, early detection and eradication, and limiting invasive plant seed dispersal into burned areas by [68,181]:

- re-establishing 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 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 St Johnswort plants and small patches adjacent to burned areas to prevent or limit dispersal into the site [68,181].

The need for revegetation after fire can be based on 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 root fragments capable of reproduction. In general, postfire revegetation should be considered when desirable vegetation cover is less than about 30% [68].

When prefire cover of St Johnswort is absent to low, and prefire cover of desirable vegetation is high, revegetation is probably not 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 necessary to detect and eradicate newly established invasives before they spread [68].

When prefire cover of St Johnswort is moderate (20%-79%) to high (80%-100%), revegetation may be necessary after fire of any severity if cover of desired vegetation is less than about 30%. Intensive weed management is also recommended, especially after fires of moderate to high severity [68].

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) [68]. See Integrated Noxious Weed Management after Wildfires for more information.

When planning a prescribed burn, managers should preinventory the project area and evaluate cover and phenology of any St Johnswort and other invasive plants present on or adjacent to the site, and avoid ignition and burning in areas at high risk for St Johnswort establishment or spread due to fire effects. Managers should also avoid creating soil conditions that promote weed germination and establishment. Weed 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 [181].

MANAGEMENT CONSIDERATIONS

SPECIES: Hypericum perforatum

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IMPORTANCE TO LIVESTOCK AND WILDLIFE:
There is no evidence in the literature that St Johnswort provides substantial food or cover for any class of livestock or wildlife. Sampson and Parker [154] indicate that domestic sheep and cattle sometimes eat St Johnswort when other forage is unavailable, and that domestic goats and deer prefer it. St Johnswort is poisonous to most livestock, particularly animals not accustomed to it and light-colored animals (see Impacts for details).

A few birds that nest in California annual grasslands were observed consuming some St Johnswort seed, but in general, birds do not appear to feed extensively upon either foliage or fruiting parts of St Johnswort. Gophers and other burrowing rodents are said to be few on heavy St Johnswort infestations as compared with their numbers on adjoining grasslands [154].

Palatability/nutritional value:

Given adequate forage most livestock avoid St Johnswort, although some grazing may occur on St Johnswort in spring when growth is young and succulent, or at other times when more palatable forage is not available [45,154]. Domestic goats and deer seem to prefer it [154].

Cover value: No information is available on this topic.

OTHER USES:
St Johnswort has a long history of use for a variety of purposes, including treatment for a variety of ailments from burns and skin disorders to depression. It has been used as an ingredient for distilling vodka, and as a source of red, yellow, purple and orange dyes. In ancient times, St Johnswort was thought to have magical properties and was used as a charm against storms, thunder, evil spirits, and witches. In folklore, it was claimed to bring good luck if sprigs of the plant were hung about the house or carried as a charm and, if you slept with them under the pillow, you would dream of a future lover [9,139]

St Johnswort is well known for its medicinal properties and a great deal of literature is available on this topic, but is beyond the scope of this review. It is cultivated in Europe as a medicinal plant and for use in the cosmetic industry [139,159,189]. Estimated international sales of St Johnswort for 1 year (1997) were between 10 and 12 billion U.S. dollars (Silber and Davitt 1998, as cited by [189]. Everett [58] includes St Johnswort in a guide to nontimber forest products of the Hayfork Adaptive Management Area, Shasta-Trinity and Six Rivers National Forests, California.

IMPACTS AND CONTROL:
Impacts: Earlier literature (e.g. [41,154,178]) seems to indicate greater impact from St Johnswort than is

currently indicated in many areas. This is perhaps due to suppression of many St Johnswort populations by introduced biological control insects (see Biological control), or to its ubiquity. In California, for example, where St Johnswort populations have been historically widespread, St Johnswort is listed as a "wildland plant of lesser invasiveness" by the California Invasive Plant Council (Cal-IPC), and as a weed that is "so widespread that the agency does not endorse state or county-funded eradication or containment efforts" by the California Department of Food and Agriculture [30]. St Johnswort occurs in 44 states and 7 Canadian provinces but is designated as noxious in only 7 states and 2 provinces [183].

In agricultural areas, St Johnswort is more of a problem in pastures than in cropland because it is controlled by regular cultivation [139]. The most commonly described impacts of St Johnswort are loss of forage production and carrying capacity on rangelands and pastures, and losses from livestock poisoning [45,143,154,178].

Hypericin, a chemical constituent of St Johnswort found at all growth stages in either fresh or dry foliage, causes photosensitization in animals that consume it. Symptoms such as blistered skin and edemas have been reported in cattle, horses, domestic sheep, and domestic goats, with goats being most resistant, and light-colored animals of all classes being the most sensitive. Horses are more susceptible to hypericin toxicity than cattle, cattle more than sheep, and sheep more than goats [19]. Livestock rarely die directly from St Johnswort ingestion; however, effects of poisoning such as blindness or swelling and soreness of the mouth may prevent affected animals from foraging and drinking, and thereby contribute to death by dehydration and/or starvation. Several authors provide more detailed descriptions of St Johnswort poisoning and conditions under which it is likely to occur [19,34,102,139,143,154,163]. Some authors (e.g. [102,139]) also suggest that St Johnswort may cause contact dermatitis in humans.

Control:

Much of the information on control of St Johnswort presented in this review comes from literature reviews and literature that provided additional pertinent ecological information.

Control of St Johnswort infestations requires several strategies designed to impact different plant parts and different stages in the plants life history. Emphasis on particular strategies may differ according to site type and St Johnswort growth habit. For example on rich soils, large St Johnswort plants with less root development may be easier to control by killing aboveground St Johnswort plant parts and then planting desirable plants, compared to the more difficult-to-control St Johnswort plants with greater root biomass in harsher sites [22,41]. With all St Johnswort control efforts, it is important that control measures are begun early and sustained for a sufficient length of time, as populations of St Johnswort can build from just a few seeds up to dense infestations in a short period of time (about 10-20 years) [25].

St Johnswort shows considerable variation in growth form, extent of vegetative reproduction, response to stress, and flowering frequency (see General Botanical Characteristics). Much of this plasticity can be related to variation in site; therefore, management strategies must be site-specific. Genotypic differences and the effects that these differences may have on susceptibility to different biological control agents have also been noted in St Johnswort ([46], and references therein).

St Johnswort seedlings are highly susceptible to competition, and the presence of competitive plant species is important to reduce the impact of periodic peaks in St Johnswort germination, establishment, and spread. Maintenance of vigorous pasture and rangeland by effective grazing management can prevent such seedling recruitment and limit St Johnswort spread. Effective grazing management plans in Australia are discussed by several authors [28,46]. In areas where vegetation is too sparse to suppress germination and recruitment of St Johnswort seedlings, other control efforts may be emphasized [22]. Any management strategy must also consider the presence of a viable soil seed bank for at least 20 years following control of St Johnswort (see Seed banking).

Based on results using detailed data from a long-term (6-7 years) observational study of St Johnswort populations, and an individual-based modeling approach for St Johnswort, Buckley and others [25] predict that the most effective management strategies for both open and shaded sites would concentrate on reducing the size of vegetative parts of St Johnswort. This may be especially true for infestations on harsh sites that tend to support St Johnswort populations with more lateral roots and root sprouts [22,41]. Single stresses, even if severe, are usually insufficient as St Johnswort root reserves respond with increased rates of sprouting from damaged roots and root crowns [22]. For example, beetles introduced for biological control defoliate St Johnswort plants but are not effective alone, especially in shaded sites (see Biological control) [25]. Multiple stresses such as defoliation and plant competition, defoliation and drought, or defoliation and fire, may cause reductions in St Johnswort crown density, and management of these factors is important for control to be successful [22,46].

Exhausting St Johnswort root reserves may require repeated stresses over a long period of time. Continuous low level herbivory through managed stock grazing may achieve this, although St Johnswort toxicity may limit grazing and a rotation of different types of grazing animals is recommended [19,28]. In its native range in Europe, crashes in population density of St Johnswort are associated with the destruction or exhaustion of root reserves by natural arthropod enemies. This has led to the current biological control strategy of targeting this part of St Johnswort's life history ([22] and references therein).

More research is needed to determine which factors affect the early stages of St Johnswort growth and recruitment, both from seed and sprouts, under different conditions, including fire treatment [25]. Whatever combinations of management techniques are adopted, a clearer understanding of the population dynamics of St Johnswort in different habitats should enable them to be better meshed together and their effects evaluated [22].

Prevention:

The most effective method for managing invasive species is to prevent their establishment and spread. Some methods of prevention include limiting seed dispersal, containing local infestations, minimizing soil disturbances, detecting and eradicating weed introductions early, and establishing and encouraging desirable competitive plants [157].

Even though St Johnswort has a widespread distribution in North America, there are many areas where it has not yet established and other areas where it remains at low densities. Preventing further introduction and spread to uninfested areas is much easier, more environmentally desirable, and more cost-effective than is the subsequent management of large-scale infestations. Some aspects of prevention include curtailment of weed development along transportation and utility corridors, inspections and cleaning of machinery and vehicles prior to their movement from weed-infested to uninfested sites, and revegetation of disturbed soils with site-appropriate plant species to inhibit St Johnswort entry. Upon discovery, pioneer St Johnswort plants should be eliminated [143]. A similar approach to St Johnswort management in National Parks in Australia is described by Knutson [105], but also includes a comprehensive biological control program for large infestations, utilizing as many available organisms as possible.

Weed inventory and monitoring are important for early detection of new infestations and prevention of spread [97]. St Johnswort colonies with as low as 30% ground cover are distinguishable from other rangeland vegetation in multispectral digital images with 0.5, 1, 2, and 4 m spatial resolution taken from airplanes. This procedure provides a method to establish baseline plant community composition and a way to monitor species population changes and dispersal over time. See Lass and others [110] for details.

Because St Johnswort infestations may be serious on overgrazed areas, adoption of grazing systems that increase or maintain cover of desirable plants and/or reduce the amount of St Johnswort seed produced is a worthwhile preventative tactic [139,154]. St Johnswort occurs along roadsides and fencerows but rarely invades "properly managed" pastures (Lane 1979, as cited by [45]).

Integrated management:

Controlling St Johnswort infestations requires more than defoliation or removal of aboveground plant parts. St Johnswort's ability to spread vegetatively and its apparent stimulation by defoliation (e.g. [41,178]) necessitate an intensive, integrated approach to control. An effective suppression program for St Johnswort requires planning, use of appropriate management methods, monitoring/evaluation, and persistence [143]. Integrated management includes considerations of not only killing the target weed, but also of establishing desirable species and maintaining weed-free systems over the long-term.

It is important to determine whether St Johnswort is a new or established invader in a particular infestation, because management approaches to each type will differ. With new infestations, emphasis may be placed upon early treatment and prevention, followed by monitoring and removal of newly established plants. Revegetation may also be useful to deter further St Johnswort invasion of the site. When dealing with an established population, the management approach may be more involved and take longer to implement. An established St Johnswort population is comprised of outlier, perimeter, and core plants. Management activities are prioritized based on plant location within the infestation. The 1st priority is management of the outlier populations to restrict continued spread of the infestation, followed by plant suppression within the perimeter and core infestation zones, respectively. Physical extraction and herbicides can be used against outlier plants [143]. A mixture of physical, cultural, chemical, and biological methods, chosen to cause multiple stresses to target plants, may be used to contain and eventually reduce perimeter and core population plants [22,143].

It is not possible or realistic to detail procedures to be followed in every potential management situation. The decision to use a combination of management methods must be based upon an assessment of plant developmental status, a characterization of sites infested or susceptible to infestation, and constraints of particular methods. Emphasis should be placed on the use of methods that interrupt St Johnswort seed dispersal and longevity, and that minimize habitat perturbations [143]. Site-specific integrated management programs can be developed for St Johnswort or other weeds ([143], and references therein).

Physical/mechanical:

Several physical methods have been used for St Johnswort management including hand-pulling or digging, cutting or mowing, tillage, mulching, and flooding. Effectiveness of various physical methods depend on age, size, and location of St Johnswort infestations. For example, St Johnswort can be effectively managed by repeated tillage in intensively cropped situations [45]; however, tillage is rarely appropriate for natural areas.

Hand-pulling or digging
of young, isolated plants is often effective, but is not considered practical for large populations of established, deeply rooted plants. Sampson and Parker [154] suggest "the mere digging, grubbing, and hand pulling of St Johnswort have proven costly and ineffective as a control measure." They observed sprouting from St Johnswort roots wherever segments were left in the surface soil, and numerous St Johnswort seedlings where adult St Johnswort plants had been dug [154]. Conversely, on prairie and dune sites on conservation preserves in Michigan, persistent annual pulling of mature St Johnswort plants to prevent seed production has been an effective control method. At Kitty Todd, Ohio, pulling is very effective, especially for early eradication of new St Johnswort populations [149]. It is important to remove as much of the root as possible, while minimizing soil disturbance, and removing all St Johnswort plant parts from the area to prevent possible vegetative growth or seed dispersal [143].

Cutting and mowing
are typically considered ineffective as management methods for St Johnswort since sprouting may occur immediately after crown removal or defoliation [34,45,149,154]. These methods may be useful for preventing seed formation in St Johnswort [143,154], by cutting 2 or more times during the growing season [143].

Repeated mowing or cutting may weaken and eventually "starve" St Johnswort plants, and thus reduce population density [41,154]. St Johnswort is particularly susceptible to defoliation in spring. In Australia, hand defoliation every 2 weeks from late April to mid-November or from mid-August to early December resulted in from 93%-98% to 87%-100% destruction of crowns in low and high density stands, respectively. Hand defoliation from mid-August to mid-November or from early October to early December killed high density stands, and reduced crown density of low density stands by 72%-92%. Hand defoliation of St Johnswort in a eucalyptus forest in Australia resulted in the death of only 45% of crowns [41]. Survival of St Johnswort plants after hand defoliation depends on the tendency of the plant to reproduce vegetatively and the life span of the individual crown [34,41]. Cutting and/or mowing may not be feasible on many sites because of inaccessible terrain and potential damage to desirable plants [143].

Cultivation/tillage:
St Johnswort is usually controlled by tillage and is not usually a problem in cultivated crops. Tillage is more effective when combined with sowing of competitive pasture or crops and adding fertilizer ([34,45] and references therein). In western Washington, St Johnswort density was reduced nearly 70% within 2 years following disking and seeding to cool-season introduced grasses (Gates and Robocker 1960, as cited by [116]).

Mulching/solarization: Sampson and Parker [154] killed St Johnswort by cutting plants to 2 inches (5 cm) above the ground surface and covering them with heavy tar paper. They did not indicate how long it took.

Flooding:
There is no literature available regarding flooding as a control method for St Johnswort, although it may be effective since St Johnswort does not thrive in waterlogged soils [154].

Fire: See the Fire Management Considerations section of this summary.

Biological:
Biological control of invasive species has a long history, and there are many important considerations before the implementing a biological control program. Tu and others [179] provide information and considerations for biological control of invasive species in general in their Weed Control Methods Handbook. Additionally, Cornell University, Texas A & M University, and NAPIS websites offer information on biological control.

There is a great deal of literature on biological control of St Johnswort in North America and Australia. The following discussion is based on literature reviews (e.g. [45,48,82,116,143]) and primary literature that discusses impacts [177], and/or population dynamics of St Johnswort and biocontrol insects in California [93], northern Idaho [31], British Columbia [84], and Australia [20,21].

Biological control of St Johnswort was initiated in Australia. A total of 12 insect species was released over 70 years, 6 of which established ([21] and references therein). Although early results were promising and led to biological control programs in other countries, including parts of North America, biological control has not yet managed to reduce St Johnswort infestations to levels that do not cause unacceptable economic or environmental damage in many areas. The Chrysomelid beetles (*Chrysolina quadregemina* and *C. hyperici*), for example, impact St Johnswort populations in certain situations, but are unable to prevent its continued spread [21].

From 1945 to 1946, shipments of both *Chrysolina* spp. were obtained from Australia and released in California. Within 2 years, both species were well established. This was the 1st attempt at control of a weed species by the intentional introduction of insects into North America [143]. Similar to initial results in Australia, *Chrysolina* spp. released in North America had a substantial impact on St Johnswort populations in many areas. In northern Idaho, the overall abundance of St Johnswort fluctuates around 3% of what was present before insects were introduced [177]. On annual grasslands in northern California, St Johnswort was reduced to less than 1% of its former occurrence 10 years after establishment of biocontrol insects [93]. The beetles were so successful in California that a 6-foot bronze statue of *C. quadregemina* was erected in the town of Eureka [129].

In some areas, however, biocontrol impacts are not as severe, and beetle populations do not reach high densities, probably due to climatic differences [116,139], particularly rainfall patterns [22]. These beetles appear to be adapted to a climate with hot, dry summers and mild, rainy winters [116], but their shade tolerance varies [20,21,24,31]. Other reasons suggested for varying impacts include predation by birds, spiders and other arthropods, and the presence of competing plant species [22].

The following table provides a list of biological control insects introduced to North America and areas where they have established. See the references listed or other reviews for more information.

Biological control agent	Locations where established	References
St Johnswort borer (*Agrilus hyperici*)	CA, ID, MT, OR, WA; mostly in mountain areas; attacks plants growing in shade	[31,142]
St Johnswort inchworm (*Aplocera plagiata*)	ID, MT, OR, WA, Canada; dry area such as rocky ground, open sandy places, and limestone regions are favored	[142]
Klamath weed beetle (*Chrysolina hyperici*)	CA, ID, MT, OR, WA; prefers conditions more moist than *C. quadrigemina*, and avoids shaded or barren, rocky locations	[31,84,142]
Klamath weed beetle (*C. quadrigemina*)	CA, ID, MT, OR, WA; mountainous, sunny and warm areas; does not seem to do well in shaded, barren, and rocky locations	[31,84,142]
Klamath weed midge (*Zeuxidiplosis giardi*)	CA, HI, OR; seems to prefer damp locations with moderate to high relative humidity and high elevations; does not seem to like dry summers, continuously windy areas, or areas heavily grazed by livestock; "ineffective" in CA, BC, and Australia	[84,142]

While no systematic release of either *Chrysolina* beetle had been made in the eastern U.S. (as of 1993), *C. quadrigemina*
has been collected from several widespread localities in New York, Pennsylvania, Maryland, West Virginia, and Ohio, since 1989. Its establishment and range expansion in the eastern U.S. apparently resulted from a natural dispersal of populations from eastern Ontario. Several other states in the East where St Johnswort occurs have not been surveyed for Chrysolinids [91].

It may be helpful to fire managers to be aware of which biological control insects may be established in their area, as this affects postfire succession and population dynamics (e.g. [20]). See Fire Management Considerations for more information.

Livestock grazing: Several authors suggest using domestic goats to graze St Johnswort-infested areas to keep St Johnswort at low densities [139,154]. Some authors also suggest that domestic sheep can be used to graze St Johnswort in a rotational grazing system [34,46,116]. In 1 example, a heavy stocking of sheep controlled St Johnswort after a fire. Sheep, however, are more sensitive to St Johnswort toxins, and heavy infestations require 2 week rotations (2 weeks on and 5 weeks off), black sheep, and special management [34]. Cattle may be more effective than sheep under some conditions as they are less sensitive to toxins [19,34,46]. Managing St Johnswort with grazing requires intensive management, as defoliated St Johnswort plants may be stimulated to sprout from roots and root crowns [178]. Also, heavy grazing may do more damage to desirable plants in some situations, thus encouraging spread of St Johnswort.

Chemical:

Herbicides are effective in gaining initial control of a new invasion (of small size) or a severe infestation, but are rarely a complete or long-term solution to invasive species management [29]. 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. See the Weed

Control Methods Handbook [179] for considerations on the use of herbicides in natural areas and detailed information on specific chemicals and adjuvants.

Based on an individual-based modeling approach for St Johnswort, Buckley and others [24] predict that herbicide control that causes a sustained reduction in survival of at least 90% would be an effective control strategy in both open and shaded sites. They, among others [34,46,143], suggest that other considerations must be taken into account when using herbicides in a control program for St Johnswort. Herbicides are often too costly to be of practical value as a management tool for extensive infestations of St Johnswort. Repeated applications are often required to achieve adequate management, small patches may be missed, the St Johnswort seed bank must be considered for up to 20 years, and potential damage to associated vegetation must also be considered, especially in natural areas. Herbicides are best used as part of a larger, integrated system, and with adequate follow-up (for example planting desirable species, and grazing management) [46,139,143]. Some authors suggest grazing prior to herbicide application to remove nontarget plant biomass that may intercept the spray [139]. Timing and rate of application are important. See specific references, product labels or extension agents for this type of information.

Several herbicides have been used in an attempt to control St Johnswort. Many reviews discuss early attempts at killing St Johnswort with chemicals, many of which are no longer in use. Herbicides found to be effective at suppressing St Johnswort include 2,4-D, glyphosate, picloram, triclopyr, metsulfuron, and fluoroxypyr [36,195].

Campbell and Nicol [36] tested several herbicides for controlling St Johnswort on a site in Orange, Australia. They compared rate and type of herbicide, timing of application, application at annual intervals, rate of water carrier, and spraying combined with sowing of improved pasture species. Herbicides tested were triclopyr + picloram, fluoroxypyr, glyphosate, glyphosate + metsulfuron, and 2,4-D amine + metsulfuron. Results indicate that the only treatment that completely killed St Johnswort was 2 applications at annual intervals in summer of fluoroxypyr. Other herbicides that "substantially" reduced St Johnswort ground cover were triclopyr + picloram, glyphosate, and glyphosate + metsulfuron. Fluoroxypyr had no effect on regeneration of annual legumes and did not damage grasses, whereas triclopyr + picloram killed legumes and other forbs, and glyphosate killed grasses. Spraying St Johnswort and sowing improved species appeared to be the best treatment for long-term control because desirable pasture species established and replaced St Johnswort. Authors conclude that St Johnswort is difficult to control with herbicides and that every effort should be made to promote successful biological control and/or effective grazing management procedures [36]. See [36] for more details.

On prairie and dune sites at nature preserves in Michigan, sponge wick application of glyphosate on cut tops of St Johnswort plants is 100% effective at controlling St Johnswort [149].

Cultural:

St Johnswort "competes strongly with other plants" but is itself sensitive to competition in the young stages or after it has been suppressed by cultivation, chemical control, or insects. If St Johnswort is suppressed by 1 or more methods but its ecological niche remains unfilled, reinvasion by St Johnswort or invasion by other undesirable species will likely occur [31,34,143]. Long-term control of St Johnswort requires that competitive plant communities be established and maintained using site-specific range management recommendations [143]. This may be especially difficult in natural areas where native species are desired [46,80].

The choice of plant species to be seeded should reflect site conditions, management, and future use. The Natural Resources Conservation Service, or local Cooperative Extension Service can recommend appropriate plant species for revegetation purposes. Small-scale plantings, evaluated for several years, provide another means to determine which plant species are most competitive with St Johnswort under prevailing climatic and land use conditions [143].

In Australia, a program of seeding pasture species (subterranean clover (*Trifolium subterraneum*) and canarygrass (*Phalaris* spp.)) combined with cultivation and fertilization on arable land, and reseeding alone on non-arable land, may control St Johnswort populations in pastures and arable rangeland [34,72]. In New South Wales and Victoria, radical land use change from badly invaded pastures to pine plantations has controlled many areas of St Johnswort because it cannot survive in densely shaded areas. St Johnswort may continue to grow along roads in the forest or plantation and may return when trees are removed [34,72]. It is usually the last species to disappear in a new forest and the first to return when the forest is cleared [34,41,72].

It is important that grazing be carefully managed before, during, and after establishment of desirable species [34,143]. Campbell [33] provides a review of different approaches to grazing management with and without seeding of improved pasture species on St Johnswort populations in heavy and light infestations on Australian pastures.

Hypericum perforatum: References

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