THE POPULATION DYNAMICS OF TANSY RAGWORT (*SENECIO JACOBAEA*) IN NORTHWESTERN MONTANA

by

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Brad David Bauer
February 6, 2006

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TABLE OF CONTENTS

TABLE OF CONTENTS-CONTINUED

TABLE OF CONTENTS-CONTINUED

TABLE OF CONTENTS-CONTINUED

LIST OF TABLES

LIST OF TABLES- CONTINUED

LIST OF FIGURES

Figure Page

LIST OF FIGURES-CONTINUED

ABSTRACT

Following the Little Wolf wildfire of 1994 in northwestern Montana, tansy ragwort (*Senecio jacobaea*) was classified as a state noxious weed. This project aimed to help prioritize the management of populations of tansy ragwort through an understanding of the biotic and abiotic factors influencing the species. Using field collected data and by constructing a prediction model, we found that the most important variables to predict the presence of tansy ragwort were distance from the main road, slope, cosine of aspect, and several remotely sensed LANDSAT ETM+ bands. Most of the predicted occurrences of tansy ragwort were within the boundary of the wildfire.

The life stage and density of tansy ragwort plants in 94 plots in several environments created by the wildfire were used to project the population growth rate after seven to eleven years following the wildfire. Using the relative invasiveness (probability $\lambda > 1.0$) of populations to prioritize environments for management, the burned and salvaged logged population had the highest probability of being invasive with probability $\lambda > 1.0$ between 0.31 and 0.24. The burned but not logged had a probability $\lambda > 1.0$ between 0.20 to 0.10 and the non-burned meadow had a probability $\lambda > 1.0$ between 0.01 and 0.00. Additionally, as the native plant populations recovered, the population growth rate and rosette survival declined.

Following a field study of the role of slashpiles in the establishment of tansy ragwort we found the highest maximum percent emergence of tansy ragwort seedlings in the low severity burn and non-burned disturbed environment of the slashpiles. The low survival of emerged seedlings and the low projected growth rates for the surviving plants indicated that the dynamics responsible for a large increase in tansy ragwort density did not occur within our slashpiles after two years.

With the addition of biological control agents to populations of tansy ragwort, the seed predator fly did not negatively affect the relative invasiveness of tansy ragwort. However, the addition of a foliage herbivore to a limited number of populations reduced the relative invasiveness of these populations.

CHAPTER 1

REVIEW OF LITERATURE

Introduction

Mack et al. (2000) suggested that non-indigenous species (NIS) threaten biodiversity worldwide. The introduction of NIS has been suggested to threaten native species with extinction by replacement in plant communities (Elton 1958, Wilcove et at. 1998). Although, there are few cases where the extinction of a NIS has been quantitatively attributed to competition with a NIS (Mooney and Cleland 2001, Sax et al. 2002), the threat has lead to large amounts of money and time directed towards prevention, control, education, and research. The U.S. Department of Agriculture's (USDA) annual budget for NIS exceeds $500 million, of which control constitutes a substantial portion (Powell 2004). However, the full economic damage created by NIS was difficult to estimate due to indirect or delayed effects (Powell 2004), and the damage caused by NIS may extend beyond economics.

Managers and scientists have increased their collaboration towards managing NIS in natural areas (Sheley and Krueger-Mangold 2003). However, the slow rate of accumulation of scientific knowledge about invasions has lead to difficulties for managers, who need to manage a potentially rapidly changing vegetation landscape (D'Antonio et al. 2004). Additionally, the invasion potential of the NIS may vary across environments; therefore, prioritization of management is important to best determine which environment(s) requires the greatest management attention. Finally, caution must be used when applying management practices because those practices could be more harmful to the environment than the presence of the target NIS.

The objectives of this thesis were to determine the environmental variables important to locating populations of tansy ragwort (*Senecio jacobaea* L.), the environmental conditions under which populations of tansy ragwort increase in density, the sources of the variability in the population growth rate (λ), the effects of burning on the establishment of tansy ragwort, and the effect of biological control agents on tansy ragwort populations for the Northern Rocky Mountain region. The results for each of the five objectives should aid decisions for management of tansy ragwort.

Tansy Ragwort

Geographic Range and History

The home range of tansy ragwort (*Senecio jacobaea*) extends from the British Isles through Europe (Harper and Wood 1957) and eastward to Asia, and Siberia (Jeffrey and Chen 1984, Bain 1991). Tansy ragwort is distributed from Greece and Asia Minor in the south to Sweden and Norway in the north (Harper and Wood 1957) ranging from near sea level in the Netherlands (van der Meijden 1974) to 1570 m elevation in Germany (Harper and Wood 1957, van der Meijden 1974). Today tansy ragwort is found in the moist, temperate maritime regions of Australia, New Zealand, South Africa, South America, and North America (Bain 1991).

Tansy ragwort probably arrived in North America from ship ballast at maritime sites (Greenman 1915) and has moved inland through contaminated straw, feed, and logging equipment (Coombs et al. 1991, Coombs et al., 1996). Tansy ragwort was first reported in the 1850s in North American in Nova Scotia, and in 1886 in Pennsylvania (Harris et al. 1971). It was recorded in western North America in 1913 on Vancouver Island, and later in Oregon in 1922 (Agriculture 2005).

Today the highest concentrations of tansy ragwort in North America occur in the Pacific Northwest (Coombs et al. 1999), where it is found ranging from British Columbia southward to northwestern California predominately in maritime regions along the coastline to the Cascade Range and with reduced abundance further inland (McEvoy and Rudd 1993a). Tansy ragwort is also found on the eastern seaboard from Newfoundland to New England (Bain 1991), and in Ontario, Canada (Harris et al. 1971). It can over winter in areas with temperatures reaching -20 ^{o}C or lower (Burrill et al. 1994).

Tansy ragwort is currently on the state noxious weed lists of Arizona, British Columbia, California, Colorado, Idaho, Montana, Nova Scotia, Oregon, and Washington (Rice 2005) (Figure 1.1)**.** The United States federal government defines a noxious weed in the 1974 Federal Noxious Weed Act as any “living stage, such as seeds and reproductive parts, of any parasitic or other plant of a kind, which is of foreign origin, is new to or not widely prevalent in the United States, and can directly or indirectly injure crops, other useful plants, livestock, or poultry or other interests of agriculture, including irrigation, or navigation, or the fish or wildlife resources of the United States or the public health” (USGS 2005).

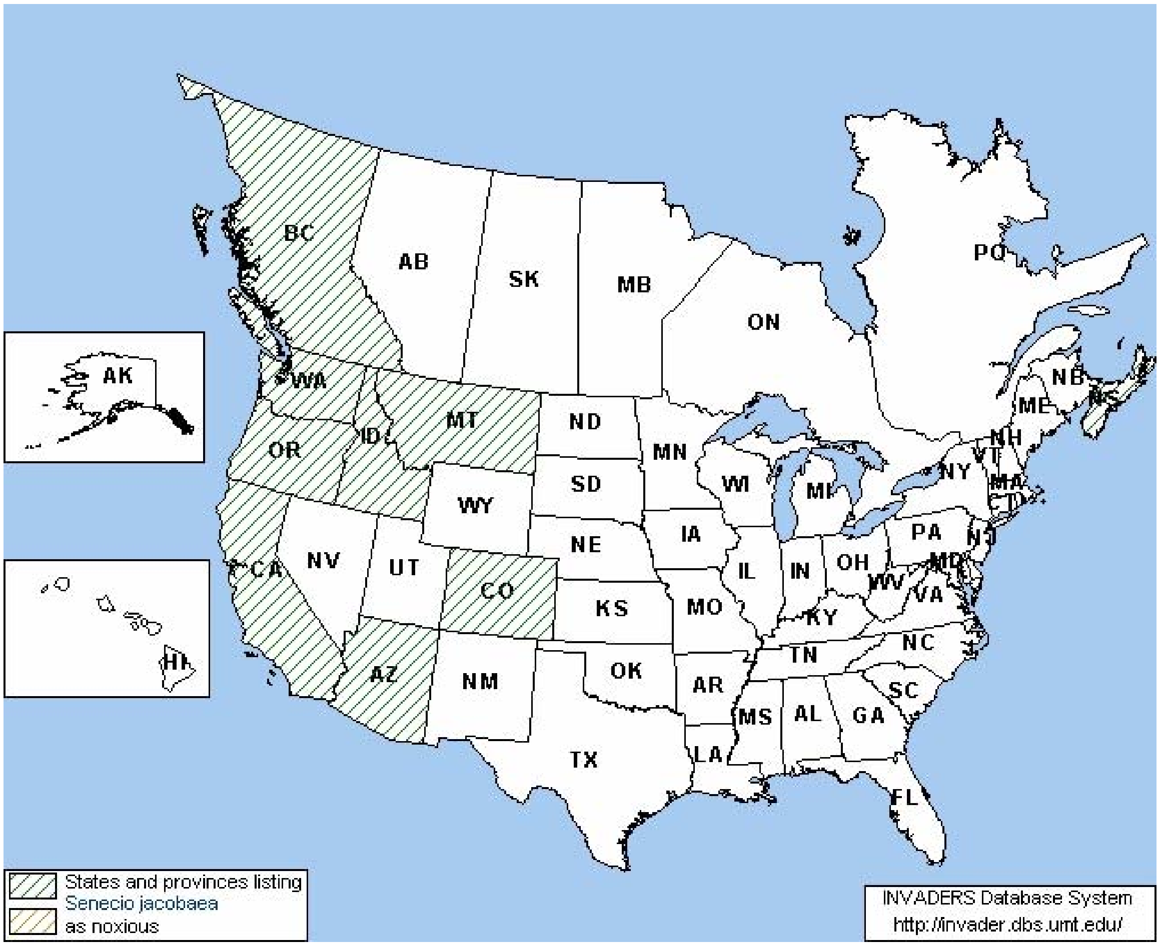


Figure 1.1. States and provinces listing tansy ragwort as noxious.

Movement of tansy ragwort into the inland Pacific Northwest was reported in 1987 with populations located in Idaho (Burrill et al. 1994). First reports of tansy ragwort in western Montana came in the 1990s (Markin 2001). Tansy ragwort was first reported in Mineral County, Montana in 1992, Flathead County in 1993, Lincoln County in 1996, and Sander County in 1998 (Rice 2005).

In northwest Montana in an area burned by the 1994 Little Wolf wildfire located in the Flathead and Kootenai National Forest a weed survey the following year (1995) found a small infestation of tansy ragwort (Richardson 1997). The level of detection in 1995 may have been reduced due to the new juveniles being in the relatively inconspicuous rosette state (Richardson 1997). In 1996 a follow-up survey of the wildfire area documented a tansy ragwort infestation of over 400 hectares of National Forest land (Richardson 1997).

Habitat

Tansy ragwort is a part of a wide range of successional / seral communities. In Britain, tansy ragwort is a late successional species present in coastal sand dune (Sharrow et al. 1988), woodland, and grassland communities (van der Meijden 1974). Repeated small scale disturbance in its native habitat allows establishment in immature juniper, hawthorn and beech series (Watt 1934, Watt 1987a). It is considered a late successional species in sand dune communities in Britain and Western Europe. However, it can be most abundant in pioneer to mid seral communities at newly disturbed sites (Harper and Wood 1957). Tansy ragwort is often found inhabiting poorly managed pastures, recently logged forests, road edges and railroad right-of-ways (Sharrow et al. 1988).

Tansy ragwort is found on many soil types including light sands, loams, clay, and alluvial deposits; but generally most common on lighter, well-drained soils (Harper 1958, Bain 1991). It is rarely found in areas with a high water table or areas with acidic soil (Harper and Wood 1957, Harris et al. 1971, Schmidl 1972, van der Meijden 1974). Soils where tansy ragwort was found in its native range have a pH ranging from 3.95 to 8.2 (Harper and Wood 1957).

Generally tansy ragwort seems to occur in a mesic habitat (Bain 1991). In Australia, New Zealand, and historically in North America it is found in areas with high annual rainfall

(Schmidl 1972, Barkley 1978, Wardle 1987). However tansy ragwort can now be found in drier eastern portion of the Pacific Northwest (Burrill et al. 1994) including eastern Washington, eastern Oregon, Idaho and Montana (Rice 1995). Tansy ragwort is found in areas of 58 - 130 cm of rain per year in England, and areas exceeding 40 - 51 cm of annual precipitation in the Pacific Northwest of North America (Harper 1958, Coombs et al. 1999). In Oregon, small infestations have been found in areas with only 30 - 35 cm of rain per year (Hawkes 1981).

Morphology

Tansy ragwort is a herbaceous species that grows from 0.3 - 2 m tall (Frankton and Mulligan 1987) and has a taproot (Bain 1991). Tansy ragwort is a biennial, winter annual or short-lived perennial, usually forming rosettes during the first year (Frankton and Mulligan 1987, Bain 1991). Bain (1991) describes the stems as being strict, erect, and arising singly or clustered from an erect caudex with branching occurring only at the inflorescence, and as the plant ages it advances from tomentose to glabrate. Tansy ragwort leaves are alternate, dark green and deeply bi- or tri-pinnatifid (Frankton and Mulligan 1987). The leaves reduce in size moving up the plant, and are 7 – 20 cm long and 2 – 6 cm wide (Bain 1991). Additionally, the leaves are broadly ovate to ovate with the rosette and basal leaves petiolate and early deciduous (Bain 1991). The middle and upper leaves, which form the flower stem, are sub sessile and weakly clasping (Bain 1991).

The inflorescences are broadly corymbiform and cymose with 20 - 60 heads (Bain 1991). Heads are usually radiate, disks 7 - 10 mm wide, with thirteen 3 - 4 mm long darktipped involucural bracts (Bain 1991). Harper and Wood (1957) found an average of 13 ray florets and 57 disk florets. Tansy ragwort achenes are heteromorphic, having different morphologies and behaviors (McEvoy 1984a).

Tansy ragwort can be distinguished from other *Senecio* species found in North America based on its large size and highly dissected leaves (Bain 1991). The western native *S. eremophilus* Richards is separable from tansy ragwort by leaf shape. Leaves of *S. eremophilus* taper to an acute point while tansy ragwort leaves are rounded (Frankton and Mulligan 1987). Additionally, tansy ragwort can be confused with common tansy, *Tanacetum vulgare* L. In the juvenile state, both plants have similar stature and flower appearance, however, *T. vulgare* lacks ligulate flowers, the pappus forms a very short crown and the leaf segments are regularly and sharply toothed (Frankton and Mulligan 1987).

Growth and Development

Once germinated and emerged, seedling mortality is high (Forbes 1977). Forbes (1977) estimated that a minimum of 57 % of germinated seeds will die as seedlings. However, previous studies with tansy ragwort show that growing vegetation and accumulation of litter can suppress germination of tansy ragwort in the field (Cameron 1935, Meijden and Waals-Kooi 1979, Crawley and Nachapong 1985, McEvoy and Rudd 1993a). Competition from surrounding plants, including grasses, may increase seedling mortality (Harper and Wood 1957). In closed grasslands tansy ragwort may not establish or compete well (Watt 1987b). Conversely, McEvoy (1984a) found that once established tansy ragwort may compete with surrounding vegetation by decreasing light under its low-growing rosettes.

Cameron (1935) found seedlings in grazed pasture vegetation, hard exposed soil, and open soil but none in long turf or short continuous turf. Similarly, van der Meijden and Waals-Kooi (1979) found tansy ragwort seedlings only in openings in the plant community. Disturbances that increase the establishment of tansy ragwort include bare soil created by moles, gophers, ants, rabbits, livestock and humans (Harper and Woods 1957).

Seedlings have smooth, uniform leaves and develop a rosette of basal leaves that have various color, shape, and hairiness (Burrill et al. 1994). Rosettes can grow up to 30 cm in diameter the first year if conditions are optimal (Harper 1958). Rosettes must reach a minimum size before flowering, with the probability of flowering increasing with size (van der Meijden and Waals-Kooi 1979). Flowering occurs during summer through autumn (Sharrow et al. 1988), usually during the second year of growth (Harper and Wood 1957). Individual rosettes typically die after flowering (Sharrow et al. 1988). Mycorrhizal associations have been documented for populations in the United Kingdom and Europe (Hawker et al. 1957, Harley and Harley 1987).

Reproduction

The disk flowers of tansy ragwort emerge first, followed by the ray flowers (Bain 1991). Once the flower is fully expanded, usually a 24 hour process, the flower is visited by many kinds of insects, especially those in the Hymenoptera and Diptera (Bain 1991). Sexual reproduction can be detrimental to the survival of the adult plants. Gillman and Crawley (1990) found that, given a few limitations, a tansy ragwort plant was more likely to survive over winter if it produced a low number of capitula for a given root volume.

In addition to sexual reproduction, tansy ragwort can reproduce vegetatively through regeneration of shoots from crown buds, adventitious buds on root fragments, and intact roots (Wardle 1987). Vegetative reproduction maybe promoted through disturbance or injury (Bain 1991), but can occur in undisturbed populations (Harris et al. 1978). Tansy ragwort has high reproductive plasticity enabling individual plants to behave as biennials, a winter annual, or as a perennial (Sharrow et al. 1988). Changes in life history often occur as a result of environment. A 1977 study found that 8 % of the tansy ragwort plants studied flowered the first year as an annual, 39 % behaved as a biennial, and 53 % acted as a perennial (Forbes 1977).

Seed Biology

Most tansy ragwort reproduction is achieved through seeds (Sharrow et al. 1988). Large variation exists in the number of capitula and seeds produced by tansy ragwort (Bain 1991). New Zealand plants averaged 1000 - 2500 capitula / plant with 55 seeds / capitulum (Poole and Cairns 1940). Plants in the United Kingdom averaged 68-2489 capitula with 70 seeds / capitulum. Australian plants averaged 75 seeds / capitula when 44 capitula were examined. Disturbance may reduce the number of seed produced. A 65 - 98 % reduction in seed production was estimated on plants that were damaged by biological control (Cameron 1935, Bornemissza 1966).

Tansy ragwort has heteromorphic seed with different morphologies and behaviors, depending on where on the flower they were produced (McEvoy 1984a, McEvoy and Cox 1987). The disk florets produce achenes that are lighter, more numerous, have a pappus, and have rows of trichomes (McEvoy and Cox 1987). Ray flowers produce achenes that are heavier, less numerous, and lack a pappus or trichomes (McEvoy and Cox 1987). The pappus of the disk achenes aids in wind transport and the trichomes aid dispersal by animal vector (McEvoy and Cox 1987).

In addition to the structural differences, the ray and disk achenes differ in dehiscence. McEvoy and Cox (1987) found that disk achenes are released shortly after maturing while the ray achenes were still on the parent plant for months after maturity. When both forms of achenes were exposed to 20 ^{o}C and 12 hour light / dark, disk achenes germinated quicker than ray, which may have been the result of the ray achene's thicker pericarp (McEvoy 1984a).

Dispersal

It was estimated that only 0.5 % of the seeds will be wind borne even with the apparent dispersal adaptations found on the disk achenes (Poole and Cairns 1940). Poole and Cairns (1940) found that 60 % of total shed seed landed within 4.6m of the base of the plants and an additional 39 % landed between 4.6 and 9m. Dispersal seems to depend more on secondary dispersal by livestock through ingestion or carried on muddy hooves or in water ways (Bain 1991). In addition to livestock, viable seeds were found in bird droppings (Salisbury 1961).

McEvoy (1984b) suggested that the two achene types can be used for different colonization strategies. The disk achenes dispersed shortly after maturing, dispersed away from the parent plant, and under favorable conditions germinated quickly, while the ray achenes remained on the parent plants for a period of months, lacked dispersal methods, and germinated slowly under favorable conditions (McEvoy 1984b). Therefore, the dimorphic seeds may enable tansy ragwort to distribute germination spatially and temporally (McEvoy 1984b).

Seed Germination and Establishment

Seeds will generally germinate in the fall or early spring (Harper and Wood 1957) but will germinate any time during the year given the proper temperature and moisture conditions (Poole and Cairns 1940). First year tansy ragwort seeds had an average germination rate of 85 % for seeds collected in the summer and 60 % for seeds collected in autumn in Australia when seeds were exposed to 12 h day / night with temperatures of 30 ^{o}C / 25 ^{o}C (Schmidl 1972). Similar germination rates were found in Washington (Baker-Kratz and Maguire 1984). Germination rates decrease for seed production on regrowth stems rather than primary shoots (Crawley and Nachapong 1985).

Tansy ragwort does not show signs of innate dormancy (Baker-Kratz and Maguire 1984). Innate dormancy includes morphological, physiological, physical, chemical, and mechanical dormancy (Silvertown 1999). However, dormancy may be triggered by vegetation cover, frost, drought, or burial (van der Meijden and Waals-Kooi 1979, Thompson and Makepeace 1983). Van der Meijden and Waals-Kooi (1979) found that temperatures from 5 ^{o}C to 30 ^{o}C are most conducive to germination. In addition, germination is found to be strongly correlated with soil surface humidity and desiccation of the soil inhibited germination (Sheldon 1974). Disturbance of the soil that brings seeds to the surface breaks dormancy caused by burial (van der Meijden and Waals-Kooi 1979), and seeds buried 1 - 2 cm below the soil surface have higher germination rates than those buried deeper (Poole and Cairns 1940). Seeds have about a 24 % viability percentage after 6 years of burial and can remain dormant for as long as 15 years (Schmidl 1972, Thompson and Makepeace 1983, Coombs et al. 1997).

Economic Significance

Tansy ragwort has an economic impact on forage production. In North America tansy ragwort is a pasture weed on both the east and the west coasts (Bain 1991). In Oregon, costs associated with forage reduction resulting from presence of tansy ragwort were estimated at $5 million annually (Isaacson and Ehrensing 1977).

Tansy ragwort contains pyrrolizidine alkaloids that are toxic to cattle, deer, horses, and goats (Goeger et al. 1981), and to a lesser extent on sheep (Wardle 1987). The alkaloids do not become toxic until broken down by enzymes in the liver during metabolism (Turner and Szczawinski 1991). The flowers are the most poisonous, concentration of the alkaloids in the leaves are half that of the flowers and the stems 25 to 50 percent the concentration of the stems (Burrill et al. 1994). The alkaloid concentration reaches peak level in the plant during June and July (Dempster 1982). Using an Ames mutagenicity test in the presence and absence of induced rat liver microsomes, some of the pyrrolizidine alkaloids have been shown to be carcinogenic, mutagenic, teratogenic, and cause lethal degradation of liver function (White et al. 1983). Additionally, the alkaloids affect butterfat production in cattle (Miller 1936), and taint honey produced by bees that have gathered tansy ragwort pollen, making the honey off-color and bitter (Deinzer et al. 1977). The toxicity of the alkaloids is not lost when the plants are dried and incorporated into the hay crop; the presence of tansy ragwort in hay can result in the abandonment of the crop (Burrill et al.1994). Howatt (1989) suggested that the alkaloids could threaten humans through contamination of the human food chain.

The economic impact of tansy ragwort is not always clear. In the immediate vicinity of tansy ragwort Wardle et al. (1995) found an increased pasture net primary productivity through the increased growth of perennial ryegrass (*Lolium perenne* L.). Additionally, Sharrow and Mosher (1982) found tansy ragwort to be a good summer food source for sheep.

Conventional Management

Sharrow and Mosher (1982) showed that intensive grazing by sheep might effectively reduce the ability of tansy ragwort to flower and produce seed. It was suggested that by reducing seed production and the death of established plants from intensive grazing, that tansy ragwort populations could be reduced to an acceptable level (Sharrow and Mosher 1982). However, Schmidl (1972) found that tansy ragwort might recover with the removal of the sheep even after 5 - 7 years of intensive grazing. Additionally, the non-selective grazing of plant competitors of tansy ragwort may lead to the maintenance of tansy ragwort populations (McEvoy et al. 1993a).

Thompson (1980) found that tansy ragwort was a poor competitor during establishment; thus, it seemed that management success could be achieved through the promotion of dense, unbroken pastureland. Recruitment from seed was lower at sites with strong competition from vigorous grass stands (Sharrow et al. 1988).

Tansy ragwort responded poorly to mechanical manipulations (Bain 1991). Damage to the plant stimulated vegetative reproduction; thus, mowing increased infestation numbers (Bain 1991) and forced the plant to perennate (Harper 1958). Regrowth originated from crowns and root buds of damaged plants (Dempster 1982). The number of plants might increase through regeneration with adequate warmth and rainfall (Dempster 1982). Yet in cool climates, Harris et al. (1978) suggested that when the carbohydrate reserves were low following defoliation injured plants were killed by frost.

Removal of the plant through pulling was only effective if root sprouting was prevented due to the removal of the entire root system or through regular cultivation (Sharrow et al. 1988). In addition to regular cultivation, cropping and sowing to pasture showed positive results in controlling tansy ragwort (Schmidl 1972).

Bain (1991) reported that hormone-like herbicides applied during seedling to rosette stages provided the best chemical control of tansy ragwort. 2, 4 D, picloram, MCPA, and 2, 4, 5 - T have been found to be effective (Coles 1967, Schmidl 1972, Thompson 1974, 1977, Black 1976, Forbes 1978, Thompson and Saunders 1984). Sodium chlorate used with or without sodium borate was used successfully to control tansy ragwort as well (Schmidl 1972). Black (1976) recommended that effective control could be achieved with herbicides applied in the spring and fall so as to catch the tansy ragwort vulnerable stages. Similarly, (Burrill et al. 1994) found tansy ragwort tolerant to herbicide during the summer months. Herbicide spray can however increase the palatability of tansy ragwort to cattle; therefore cattle should be excluded from a sprayed pasture for several weeks (Irvine et al. 1977, Bain 1991) to reduce the exposure of grazing cattle to alkaloids contained in tansy ragwort.

Biological Control

The aim of biological control is to reduce and maintain tansy ragwort populations below an economic threshold (McEvoy et al. 1993a). Over sixty species of natural enemies are known present in tansy ragwort's native habitat (Cameron 1935). Three insects have been studied as biological controls for tansy ragwort populations in the United States: the ragwort seed head fly (*Pegohylemia seneciaell* Meade), the flea beetle (*Longitarsus jacobaeae* Waterhouse) and the cinnabar moth (*Tyria jacobaeae* L.) (Watt 1987b).

The ultimate goal of introducing biological controls is to reduce the population size of tansy ragwort to a level that is no longer economically detrimental (Burrill et al. 1994). The intent of releasing biological control agents is not removing every individual tansy ragwort plant. Yet, McEvoy et al. (1993a) found that on the Oregon coast, once the biological control agents are established, a process of successional development followed that favored plant species other than tansy ragwort. The populations of biological control agent are maintained over a global scale even though the biological controls interactions with tansy ragwort doomed them at a local scale (McEvoy et al. 1993a).

Ragwort seed head fly (*Pegohylemia seneciaell* Meade) looks like a housefly and is active in early summer (Burrill et al. 1994). The female seed head fly deposits her eggs among the florets or bracts of a tansy ragwort flower head (Burrill et al. 1994). The eggs hatch in three to four days and the larvae pierce up to 40 percent of the ragwort seed heads to feed for several months on the developing seeds in a process that consume 75 to 95 percent of the seeds (Burrill et al. 1994). Mature larvae will then enter the soil to pupate and over winter (Burrill et al. 1994). The seed head fly is not an effective biological control by itself (Burrill et al. 1994)

The ragwort flea beetle (*Longitarsus jacobaeae* Waterhouse) has been established in British Columbia, California, Oregon, and Australia (Bain 1991). In California and Oregon; the established populations of the ragwort flea beetle alone have not fully reduced the population size of tansy ragwort (Bain 1991). However, populations of tansy ragwort were strongly suppressed west of the Cascades Mountains by just the flea beetle, leaving the ragwort seed fly and the cinnabar moth to play a lesser role as biological control agents (McEvoy et al. 1991, Turner and McEvoy 1995). McEvoy et al. (1993a) found that the flea beetle is nearly monophagous on tansy ragwort and effectively searches for and colonizes new populations. The flea beetle attack tansy ragwort at both the adult and larval stage. During the larval stage, the beetle causes damage by defoliation of tansy ragwort plants and partially decapitated the plant resulting in floral abortion (Binns 1976) or attacks the roots (Frick 1970). This “grazing” of tansy ragwort may lead to the elimination and replacement of tansy ragwort by its competitors (McEvoy et al. 1993a).

Since 1950 the cinnabar moth (*Tyria jacobaeae* L.) has been successfully established at sites around the world (Bain 1991). The adult moth is about one inch long, black and red, has distinguishing black and yellow or orange bands, and is active in early summer (Burrill et al. 1994). A female moth deposits 100 to 300 yellow eggs in about forty clusters on the underside of leaves (Burrill et al. 1994). After 1 to 3 weeks the eggs hatch and the larvae feed on leaves, bud, and flowers and often defoliated all of the tansy ragwort plants in the area (Burrill et al. 1994). Larvae pupate in the soil or under debris and remain inactive until the following spring (Burrill et al. 1994).

Schmidl (1972) suggested that cinnabar moth was detrimental to tansy ragwort by damaging the plant's flowers and stems, which results in reduced seed production and seed viability but not the overall plant population numbers. Prins and Nell (1990) found that the herbivory of tansy ragwort by the cinnabar moth reduces seedling establishment and rosette growth, shortens flowering stems and increases ragwort mortality. However, even tansy ragwort plants that have been defoliated can produce new shoots that are capable of producing substantial number of seed under suitable conditions (Islam and Crawley 1983). Yet, the seeds produced by the new shoots following defoliation weigh less than seed produced on plants not attacked by cinnabar moth (Islam 1981, Nachapong 1983). Reduced seed size reduces tansy ragwort fitness (Crawley and Nachapong 1985). Additionally, if seed production on the regrowth is late in the growing season and autumn conditions are moist, the pappus might fail to dry out, which could reduce seed dispersal (Crawley and Nachapong 1985). Van der Meijden (1979) concluded that even during years when tansy ragwort was defoliated up to 90 % by the cinnabar moth, the negative effects of the cinnabar moth on tansy ragwort were small compared to other factors (e.g. environmental conditions).

Following the release of the cinnabar moth, a population of tansy ragwort will eventually reach a new equilibrium (Bain 1991). Additionally, Fuller et al. (2001) found that cinnabar moths in the field used other *Senecio* species including the native species, *S. triangularis* and *S. pseudaureus* in North America.

Nearly complete control of tansy ragwort could be achieved through the release of the flea beetle in conjunction to the release of the cinnabar moth (Hawkes 1981). Control of tansy ragwort through the combined action of the cinnabar moth and the flea beetle in two California coastal prairies improved productivity of two California pasture sites (Pemberton and Turner 1990). Additionally, non-indigenous perennial grasses replaced controlled populations of tansy ragwort in Oregon (McEvoy et al. 1991). The synergistic effect of the combined release may be because the minimum threshold tansy ragwort population size for colonization by the ragwort flea beetle is lower than that for cinnabar moth allowing the flea beetle to attack lower density populations of tansy ragwort (McEvoy et al. 1993a). Additionally, the beetle and the moth attack the host at different times of the year (McEvoy et al. 1993b). The combined damage to tansy ragwort by the moth and the beetle have a greater effect on seed production than the sum of their independent effects (McEvoy et al. 1993a). However, McEvoy (1994b) found that the addition of the flea beetle to a tansy ragwort-cinnabar moth interaction quickened the elimination of tansy ragwort while adding the cinnabar moth to a flea beetle-ragwort interaction did not accelerate the elimination of tansy ragwort. McEvoy (1994b) found replacement of tansy ragwort by its competitors increased when exposed in order of: the moth, the flea beetle, and both the moth and beetle.

Cinnabar moth and the ragwort flea beetle have varying effectiveness on different populations of tansy ragwort. McEvoy et al. (1993a) suggests that reduction in the fecundity of tansy ragwort populations through attack by cinnabar moth and flea beetle regulates the population numbers of tansy ragwort when recruitment was seed limited. However, when the recruitment of tansy ragwort was controlled by changes in open space (e.g. undisturbed, mesic grassland), reducing fecundity through biological control (herbivory) had no effect on population numbers (McEvoy et al. 1993a).

Several fungi have been associated with tansy ragwort, one of which is *Puccinia expansa* Link (Harper and Wood 1957). *Puccinia expansa* attacked and deformed the leaves and the flowering stems of the tansy ragwort (Alber et al. 1986). Alber et al. (1986) studied the suitability of *Puccinia expansa* as biological control and found in greenhouse conditions that dry mass of tansy ragwort was reduced by 60 % after they inoculated on six occasions at 2-week intervals. Alber et al. (1986) concludes *Puccinia expansa* was specific enough to be used as a biological control agent for tansy ragwort and *Senecio alpinu*, while other related *Senecio* species were only slightly affected or not at all.

Response to Burning

The reports of the use of fire as a management tool for tansy ragwort are unclear from the published literature; however, fire may serve as a disturbance that enables the establishment or increased density of tansy ragwort in the intermountain western United States. Poole and Cairns (1940) found that flamethrowers can effectively kill a reproducing plant and destroy the viability of attached seeds. However, Mastroguiseppe et al. (1982) conducted several control burns at an infested site in Redwood National Park, California with inconclusive results.

Tansy ragwort may respond with increased density following fire. A wildfire at Tally Lake Ranger District of the Flathead National Forest in Northwest Montana fire created ideal conditions for tansy ragwort seedling emergence (Richardson 1997). As cited by the Final

Environmental Impact Statement (FEIS) for the Tansy Ragwort Control Project in the Flathead National Forest of Northwest Montana, tansy ragwort populations existed in the Tally Lake Ranger District before the Little Wolf Fire of 1994 (Richardson 1997). In 1995 a study showed that populations of tansy ragwort within the burn had decreased (Richardson 1997). However, this apparent decrease may have been the result of juvenile plants in the small, inconspicuous rosette stage. In 1996 an infestation of over 400 hectares, mostly of which had been burned in the Little Wolf Fire, was recorded (Richardson 1997).

Tansy Ragwort in Northwest Montana

Tansy ragwort was first discovered in the Flathead National Forest in Flathead County in 1993. Tansy ragwort seeds may have been arrived to these sites on logging equipment from Oregon (Richardson 1997). In 1994 several wildfires, including the Little Wolf wildfire occurred in northwestern Montana. The Little Wolf fires burned approximately 4,000 hectares within the Tally Lake Ranger District in the Flathead National Forest and an additional 2,000 hectares in the adjacent Fisher River Ranger District in the Kootenai National Forest. Surveys conducted in subsequent summers located populations of tansy ragwort in both the Flathead and Kootenai National Forest. Tansy ragwort was discovered colonizing areas burned by the 1994 wildfires (Richardson 1997) as well as unburned patches of meadow. Due to the use of the these areas for cattle grazing and studies showing the toxicity of tansy ragwort to livestock and some wildlife (Goeger et al. 1981, Wardle 1987), these new populations were of particular interest.

Because tansy ragwort was thought to be limited to maritime climates, the Montana sites were considered resistant to invasions of tansy ragwort, due to their higher elevation and low annual temperature, soil moisture, and air humidity (Table 1.1).

Table 1.1. Mean (± standard deviation) climate data for the period of 1949 to 2005 for Libby 32 SSE Montana weather station near Little Wolf Creek study site. Data was obtained from the Western Regional Climate Center.

Mean annual temperature (°C)	Mean annual maximum temperature (°C)	Mean annual minimum temperature (°C)	Mean annual precipitation (cm)	Mean annual snow fall (cm)
4.78 (1.00)	11.94 (10.11)	-2.38 (5.64)	62.86 (1.72)	267.46 (25.25)

Primary Objectives for the Project

Tansy ragwort was classified as a noxious weed in Montana following the Little Wolf wildfire. The terms weed, exotic, non-native, invasive, invader, alien and non-indigenous species are often used interchangeably when people are mapping or discussing plant species that they do not want to observe in their management area. The terms have slightly different connotations to different people and some terms are more emotive than others, but all of the terms are generally used to refer to a plant species that is occurring in an area where it was not observed prior to the influx of white settlers or agricultural mechanization. For ease of reading we have generally used the term non-indigenous species (NIS).

At the crudest level the term weed defines a species that is growing where someone has defined that they don't want it to, even if it is indigenous to that area. While most species listed on County, State or Federal Noxious Weeds lists are non-indigenous to the area a very few which are indigenous. This means that the term non-indigenous is incorrect in a small number of cases but this does not affect the validity of the different inventory/survey methods described.

The only term listed above that we have not and would caution against using as a general term is “invasive”. We define an invasive species as a NIS that is known as results of monitoring efforts to consistently increase in density and / or spatial extent. A designation of invasive under this definition does not imply impact to the ecosystem of the native population or meta-population (Rejmánek et al. 2002).

This project aimed to help prioritize the management of tansy ragwort populations through an understanding of influential biotic and abiotic factors (Figure 1.2). This prioritization goal was investigated with five objectives: (1) determining the probability of occurrence of tansy ragwort across a range of environments; (2) determining under what environmental conditions, following the 1994 Little Wolf Fire, tansy ragwort presented the greatest threat of invasion; (3) identifying the sources of λ variability; (4) determining the role of slashpiles for the establishment of tansy ragwort; and (5) determining how the demographics (transition between life history states, seed production and vegetative reproduction) of tansy ragwort respond to the addition of biological control agents (cinnabar moth (*Tyria jacobaeae*), and ragwort seed fly (*Botanophila seneciella*)).

Objective 1: Spatial Modeling

Management methods for NIS can be improved by understanding the relationship of a NIS distribution to environmental variables. If the occurrence of a NIS is correlated with a variable, then the sample area can be stratified to improve the probability of finding the particular NIS (Hirzel and Guisan 2002). Due to high cost of conducting surveys, stratification on a know correlated variable may improve the probability of locating the NIS and models of species distributions and richness can be generated (Turner 1989).

The integration of modeling with a geographical information system (GIS), allows the extrapolation of species distributions across large regions (Ferrier et al. 2002). GIS enables the use of digital elevation maps (DEM), which form the basis for the generation of new maps of environmental variables, and determines the spatial resolution of the derived maps (Guisan and Zimmerman 2000). The basic products of the DEM are slope, aspect, topographical position, and curvature (Guisan and Zimmerman 2000).

Statistical modeling in conjunction with GIS allows biological distributions to be extrapolated to non-surveyed parts of the region by modeling the relationship of available biological survey data and remotely sensed environmental layers (Ferrier and Smith 1990). The probability maps provide knowledge that can reduce the need for difficult and expensive inventories, while gaining an understanding of the variable(s) driving the occurrence of the NIS, and help managers predict the probability of occurrence of populations of NIS.

One of the earliest applications of GIS modeling used the generalized linear model (GLM) and GIS to model the species distributions of the rufous scrubbird (*Atrichornis rufescens)* in relation to field survey data of climate, terrain, and vegetation variables in Australia (Ferrier et al. 2002). More recently, Rew et al. (2005) used GIS and statistical modeling to model the presence / absence of three NIS in the northern range of Yellowstone National Park in the USA.

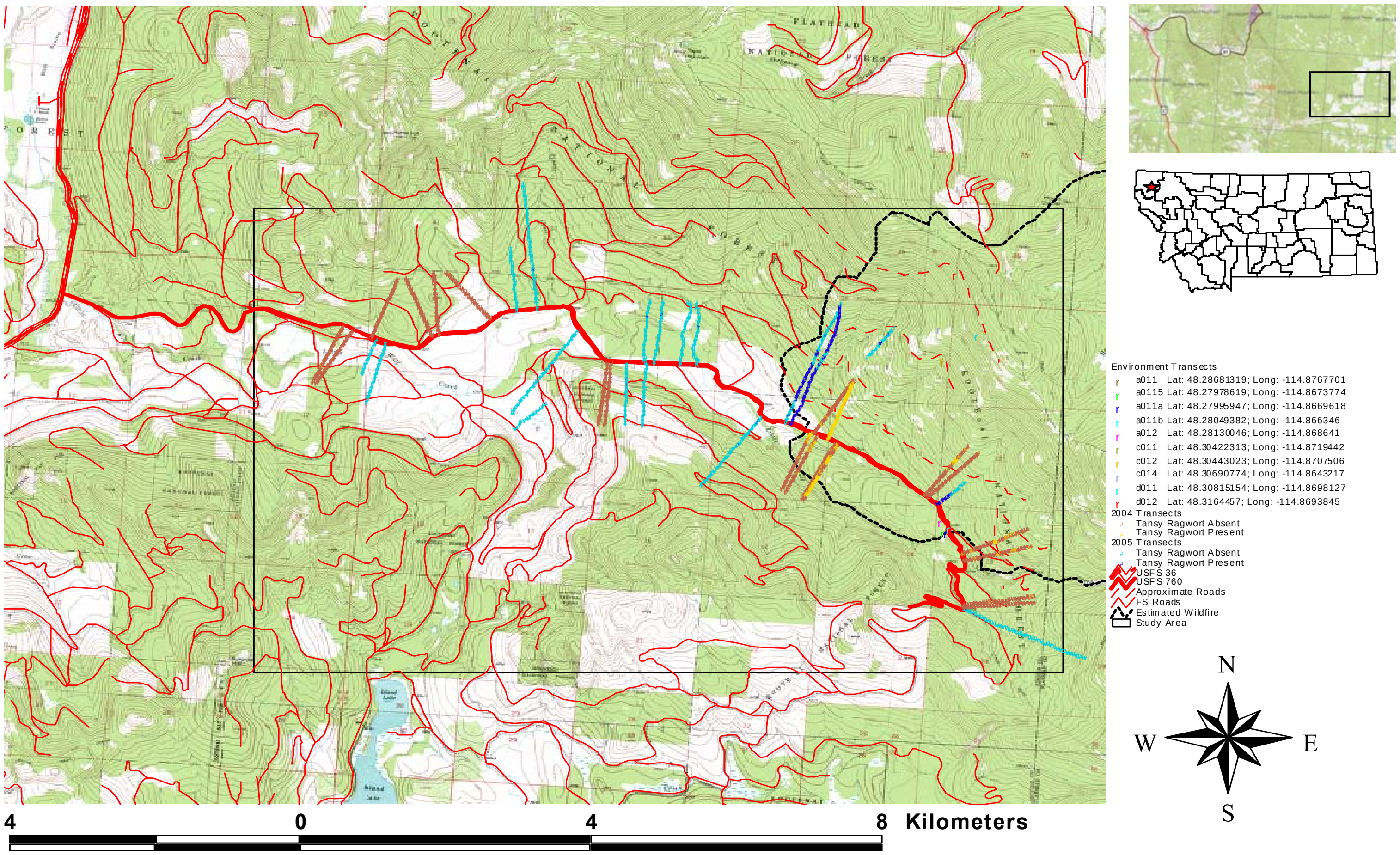


Figure1.2. Location of survey transects, study area (Chapter 2) and environment transects (Chapter 3) (Appendix G).

Objective 2: Population Growth Rates

Transition Matrix Models for Plant Populations. Plant population models can be used to gain an understanding of the biology of invasion and to focus management strategies (Shea and Kelly 2004). Models organize information about a NIS as well as identify areas where additional information is needed (Maxwell et al. 1988). Demographic models have enabled the integration of impacts of management on life-history stages into measures of population performance (Thomson 2005). Thus, demographic models are important tools in conservation and management (Caswell 2001).

Leslie (1945) and Lefkovich (1965) first developed matrix models as tools for animal population studies. Leslie (1945) developed age structured matrix models whereas Lefkovich (1965) developed a stage structured matrix model. The matrix approach to model perennial plant populations was first used by Sarukhan and Gadgil (1974). A stage-structured model is useful, because rarely is the age of an individual known (Lefkovich 1965). Additionally, stage structured models characterize plant populations well because of size-dependent demography in plants (Caswell 2001).

Matrix models have facilitated the analysis of population dynamics of species with complex life cycles (Leslie 1945), by enabling changes in population size to be a function of both population size and structure (Lotka 1925). Population is defined as the distribution of individuals in different life history stages, size classes, developmental, or functional stages (Sarukhan and Gadgil 1974). The stages of a population includes plants at different ages or definable states, such as immature plants and reproducing mature plants. Individuals of the same species could vary in life history due to demographic parameters being a function of the individual's age, size, developmental state, or a combination (Werner and Caswell 1977, de Kroon et al. 2000).

The population density depends on the rate at which individuals mature into another stage or die (Maxwell et al. 1988). In this study the total population densities N_t were defined as the number of individuals per m^2 in each stage or state at a specified time (t), and were shown in the matrix models as a column vector that contained the numbers of individuals in each stage or state. The probably of survival for each stage or state from one time (t-1) until the next (t) was summarized in a 'projection' or 'transition' matrix (Cousens and Mortimer 1995).

Through the repeated multiplication of the transition matrix with the vector of the number of individuals in each class, the λ converged asymptotically to a constant that equals the dominant eigenvalue (λ) of the matrix (Cousens and Mortimer 1995, de Kroon et al. 2000). The changes in the λ for tansy ragwort were monitored with the dominant eigenvalue λ (de Kroon et al. 2000, Caswell 2001). For our study, a population with a $\lambda > 1$ is defined as an locally increasing or invasive population, a population with a $\lambda = 1$ is a stable population at equilibrium, and a population with a $\lambda < 1$ is in decline or showing a trend toward local extinction. By definition, the left eigenvector equaled the stage reproductive value distribution while the right eigenvector was the stable state distribution (de Kroon et al. 2000). Additionally, the projected population dynamics were used to measure the elasticity, which indicated the relative contributions of the transition matrix element to the overall λ (Cousens and Mortimer 1995, de Kroon et al. 2000, Caswell 2001).

These growth rates are projections rather than a forecast or prediction (Caswell 2001). A forecast identifies what will happen, a prediction predicts what will happen given the limits of the data, and a projection describes what would happen given certain hypotheses (Caswell 2001). Calculated λ are projections due to the matrix model assumptions requiring that (1) age or stage specific survival rates are the same from year to year, and (2) recruitment into the population is constant from year to year (Watkinson 1986).

Matrix Models as Tools. Matrix models have been used for the last thirty years in conservation biology and can accommodate many types of life histories (Caswell 2001). Matrix models are relatively simple and provide information about whether a population was growing or declining (Shea and Kelly 1998).

Though time consuming, the use of site-specific or year-specific matrices can reveal patterns in finite rates of increase, natural variation in finite rates of increase and elasticities, and the relationship of demography to environmental gradients (Menges and Quintana-Ascencio 2004). These relationships can help identify the “Achilles heel” of the target species (Harper 1958), address questions of how management could target particular life-history stages (Crouse et al. 1987), and evaluate the effectiveness of control methods, including biological control (Maxwell et al. 1988, Shea and Kelly 1998, McEvoy & Coombs 1999, Parker 2000, D’Antonio et al. 2004). In addition, stochastic growth rates and sensitivity could be estimated for models requiring temporal variance in demographic rates (Thomson 2005).

A matrix model was used to model the impact of introduced biological control agents and other management strategies on nodding thistle (*Carduus nutans* L.) in New Zealand (Shea and Kelly 1998). Knowing the modeled impact of the biological control agents, managers can prioritize which biological control agent to release or to focus redistribution (Shea and Kelly 1998). A matrix model of leafy spurge (*Euphorbia esula* L.) was used to identify weak points in the vulnerable stages and understand regulation of population growth (Maxwell et al. 1988).

However, models can be uncertain (Pascual et al. 1997). Errors can occur with the omission of parameters that could be important to population dynamics, and the inclusion of parameters that are not necessary but alter population dynamics (Peters 2004). Additionally, dynamics may involve complex interactions among life stages not adequately captured in the matrix model (Tuljapurkar and Caswell 1997) and thus the results of these models should be viewed with caution (Soehartono and Newton 2001).

The importance of a long-term approach for parameterization when using matrix models has been stressed because data from a few years might fail to capture the variation in the population parameters (Bierzychudek 1982, Shea and Kelly 1998). Additionally, transition values must be calculated carefully for the natural variance in λs might be masked if transition matrices are built using mean demographic parameter values (Menges and Quintana-Ascencio 2003).

Difference Equations. Population matrix models are derived from the perceived life cycle structure (e.g. Figure 3.1) that represents the important states of an organism (Leslie 1945). Another method to project λs uses a series of difference equations rather than matrix algebra. The difference equations are solved in succession to obtain the λ (Hubbell and Werner 1979). The general form of the difference equations is:

$$X_t = X_{t-1} + (\sum MI_{t-1} - \sum MO_{t-1})\,\Delta t, \qquad \text{Eq. 1.1}$$

Where X_{t-1} represented the variable of stage or state variable X at time t-1, and $\sum MI_{t-1}$ and $\sum MO_{t-1}$ represented the sum or the values entering X and leaving X during the time interval (Martinez et al. 2005).

In our study difference equations were used to calculate the growth rate when a stable state was reached. The stable state was the generation when the proportion of mature plants became stable from generation to generation. With the use of the difference equations, we defined λ as the ratio of population size at the current time (n_t) to population size at the previous time (n_{t-1}). The population size was defined as the number of rosettes and flowering plants per population (1.0 m^2) in the fall census. Like the matrix modeling approach, the λ for the difference equations was defined as locally increasing or invasive if $\lambda > 1$, stable or at equilibrium if $\lambda = 1$, in decline or heading to local extinction if $\lambda < 1$. In addition, λ provides a continuous measure of population relative invasiveness and thus can be used for prioritization of NIS populations for management.

Population Viability Analysis (PVA). Population Viability Analysis (PVA), commonly based on the matrix methods (Menges 2000), can be used as a formal framework to investigate the effects of management strategies on population viability (Beissinger and Westphal 1998) and to predict the fate of the future population (Caswell 2001). PVA has been used in both animal and plant investigations.

The use of PVA has been well developed for the assessment of threatened and endangered species. PVA has been used to estimate the future size of a population (Boyce 1992, Lacy 1993, Brook et al. 1997, Brook et al. 2000), measure the risk of population extinction (Boyce 1992, Brook et al. 1997, Brook et al. 2000, Ellner and Fieber 2003), to assess management strategies (Lindenmayer and Possingham 1996, Ellner and Fieber 2003), to investigate the assumption about regulating mechanisms of population dynamics (Lindenmayer et al. 1995), and to measure the finite rate of increase (λ) of a population (Menges 2000). PVA has been often expressed as probabilities of population growth or decline over a specified time length (Beissinger and Westphal 1998).

Typically PVA has been utilized in the exploration of the consequences of management strategies, time, and / or natural perturbations, to the viability of a threatened or endangered population. PVA can also be used to assess the invasiveness of populations of NIS. PVA was used in this project to assess the invasiability of populations of tansy ragwort. We are terming our use of the methods of PVA as population invasibility analysis (PIA). With the use of PIA we sought to identify the environmental conditions where tansy ragwort was the most invasive and the relative effect of biological control agents on invasiveness.

Through the use of PIA in combination with the life history model, the potential invasiveness of tansy ragwort in different environments was assessed enabling management prioritization of tansy ragwort populations based on environment and the success of the biological control agents. The specific environments were created in part by the Little Wolf wildfire of 1994 and subsequent salvage logging and include: 1) areas burned in the wildfire, 2) areas burned in the wildfire and later salvaged logged, and 3) a non-burned meadow.

Critiques of PVA. A major problem with using PVA and PIA for conservation biology and invasion biology is that decisions often need to be made quickly (Ellner and Fieberg 2003). Therefore, the data may be adequate to parameterize a simple PVA model, but estimates of parameters might be imprecise and uncertain (Ellner and Fieberg 2003). Inference space is also often limited by lack of replication and a complete selection of environments where populations may exist (Beissinger and Westphal 1998). Additionally, care must be taken to ensure the inclusion of the important aspects of a species' life history, not just the ones that are easy to observe, in the selected or constructed species model (Peters 2004). Different model structures can lead to different conclusions (Pascal et al. 1997). Coulson et al. (2001) pointed out that for a PVA to accurately predict future dynamics, the future λ would need to be similar to that recorded during the data collection period. Yet, Caswell (2001) suggested that this uncertainty could strengthen the PVA through incorporating bootstrap or Monte Carlo uncertainty analysis into the analysis process. These concerns suggest that the conclusions drawn from PVA models cannot be relied on. However, generalizations about the relative importance of different transitions in the life cycle are probably most sound and the λs should be viewed as expressing trends rather than specific values (Caswell 2001).

Given the problems with data collection and with interpretation, the popularity of the use of PVA does not always reflect the reliably of the results (Ball et al. 2003). As with any model, PVAs are a simplification of nature and thus only a representation of reality (McCarthy et al. 2001, Caswell 2001).

Sensitivity and Elasticity Analysis. Sensitivity analysis and elasticity analysis have been used to assess changes to the growth rate (λ) due to future alterations to the population size or vital rates (Caswell 2001). In this manner a PVA model enables the assessment of the effect of changes to model parameters on the output of interest (Burgman 2000).

Sensitivity analyses are conducted by changing a value of a parameter representing a transition rate in the matrix model while keeping all other parameters constant (Maxwell et al. 1988). With changes to the transition rate, the variation in the output is noted (Drechsler and Burgman 2004) and the sensitivities interpreted as the slope of the λ as a function of the changed transition (Caswell 2001). Sensitivity analysis quantified the absolute change in the growth rate due to an infinitesimal absolute change to a matrix transition (de Kroon et al. 2000). Sensitivity values were calculated as:

$$\text{Sensitivity values} = \frac{\Delta output / output}{\Delta parameter / parameter} \quad \text{(Maxwell et al. 1988).} \qquad \text{Eq. 1.2}$$

Sensitivity analysis is useful for investigating the effects of additive perturbations to transition rates (Caswell 2001). A large sensitivity value indicates that small adjustments in a transition created large changes in the model (Maxwell et al. 1988). However, sensitivity analysis was not useful in comparing the contribution of transitions within a matrix to the λ (de Kroon et al. 2000).

Elasticity analysis was used to find the proportional contribution of each matrix parameter or vital rate to the growth rate (λ) (Caswell 2001). Elasticity was the slope of the log of the growth rate (log λ) as a function of the log of the vital rate (Caswell 2001). When all of the remaining elements of the transition matrix were held constant, elasticity analysis quantified the relative change in the λ due to small relative changes to the matrix transition elements (de Kroon et al. 2000). Elasticities were calculated as:

$$\text{Elasticity values} = \frac{\lambda}{\Delta parameter} \times \frac{parameter}{\lambda} \qquad \text{Eq. 1.3}$$

Conservation biologist have utilized elasticity values to quantify the relative importance of matrix elements to the λ (de Kroon et al. 2000). Elasticity values are useful to investigate the effects of proportional perturbations to vital rates (Caswell 2001). Elasticities have been used to examine effects of management practices of NIS (Shea and Kelly 1998).

Additionally, the elasticities of the growth rate always sum to one (de Kroon et al. 1986), permitting the comparison of the relative importance of transitions within the life cycle (de Kroon et al. 2000). Comparisons of elasticities are possible between individuals of a population or between different species with similar or very different growth rates (de Kroon et al. 2000).

Objective 3: Population Growth Rate Variability

The role of available resources for the establishment of NIS has been debated (Tilman

2004, Stohlgren 2003). Plants need to obtain the required resources for survival from the environment. However, plant species differ in survival and success across gradients of these resources (Tilman 1991) and, use different strategies of resource need and use (i.e. ruderal, competitive, and stress-tolerant species) (Grime 2001).

Competition for resources can be between individuals of the same species (intra-specific) and between individuals of different species (inter-specific). Density dependence has frequently been observed in plant populations (Buckley et al. 2001). Density dependence has been incorporated into models of plant populations (Maxwell et al. 1988) to make stage-classified population dynamics more realistic, by influencing growth to be nonlinear and avoiding exponential growth (Neubert and Caswell 2000).

Density dependence is the result of plant competition for available resources. The resources needed by plants are dispersed heterogeneously within and across environments. Therefore, local conditions might be more favorable to the establishment and growth of one plant species than another. This spatial heterogeneity of resources levels can account for the variation of λ of plants of the same species within and across environments at one time. The addition of temporal heterogeneity of the resources in the environment can also help further explain the variability in the λ.

Objective 4: Role of Slashpiles

The harvest of timber results in woody debris that is unsuitable for use as lumber. Similarly, thinning of small diameter trees for “ecological reasons” creates large quantities of unwanted wood, termed slash. Frequently the slash produced in either situation is gathered into large piles near roads and removed through chipping or burning (Smith et al. 1997). Burning of slash in piles near roads is favored, for it enables land managers to safely burn under a broad range of weather conditions (Hardy 1996).

Anecdotal evidence suggests that the burning of slash can assist the spread and establishment of NIS and ruderal plant species (Dickinson and Kirkpatrick 1987). However, very few studies have quantified the effects of burning slashpiles on NIS establishment. Additionally, the conflicting results from the few existing field studies of slashpile burns and controlled laboratory studies limit the usefulness of this information for land managers.

The need for understanding the effect of slashpile burning on the ecosystem will likely gain attention in the growing atmosphere of concern about NIS effects on ecosystems, and as areas of early detection and rapid response. Learning the effects of slashpile burning on the forest ecosystem can help assess when and where to use slashpile burning as a management tool.

Objective 5: Population Dynamics with Biological Control

The aim of biological control is reducing and maintaining populations of NIS below an economic threshold (McEvoy et al. 1993a). Biological control of NIS should be improved with developments in the ability to predict the population dynamics of plant populations under herbivory, and plant compensation capacity (Cox and McEvoy 1983). Knowing the dynamics of the target plant population should help select biological control agents that target weakness in the life history of the plant populations and help determine which biological control agents to focus redistribution (McEvoy and Coombs 2000).

Modeling the interaction of the biological control agent and the target NIS might highlight the importance of proceeding with caution with introductions of biological control agents. Once a control organism has been released the introduction is generally irreversible (McEvoy and Coombs 2000). It is important to know whether the biological control agents are both effective and ecologically safe (Louda and Stiling 2004). However, predicting indirect interactions of the biological control agents and species other than the target NIS is not easy (Strauss 1991).

Summary

This thesis contains six chapters; the first introduces my subject species, tansy ragwort, the other five focus on populations of tansy ragwort in the Little Wolf drainage. Chapter two of this thesis focuses on predicting the occurrence of tansy ragwort populations according to correlations with environmental variables. Chapters three and four focus on projecting and understanding the variability of the tansy ragwort population growth. Chapter five investigates the common anecdotal suggestion that slashpiles serve as locations for introduction and expansion of tansy ragwort populations. Finally, chapter six focuses on the role of a seed predator and foliage herbivore on the population dynamics of tansy ragwort. These studies where performed in an environment previously thought to be resistant to invasion by tansy ragwort. This work seeks to understand where populations are located, if they are invasive, and how to prevent new and control existing introductions.

CHAPTER 2

DETERMINING THE DISTRIBUTION OF TANSY RAGWORT ACROSS A RANGE OF ENVIRONMENTS

Introduction

In the Pacific Northwest, tansy ragwort (*Senecio jacobaea* L.) ranges from British Columbia southward to northwestern California, predominately in maritime regions along the coastline to the Cascade Range and with reduced abundance further inland (McEvoy and Rudd 1993). In addition to the Pacific Northwest coastline, tansy ragwort is found on the eastern seaboard from Newfoundland to New England (Bain 1991), and in Ontario, Canada (Harris et al. 1971).

Tansy ragwort is most commonly found in mesic habitats (Bain 1991). In Britain, tansy ragwort is a late successional species present in coastal sand dunes (Sharrow et al. 1988) in woodlands, and in grassland communities (van der Meijden 1974). Repeated small-scale disturbance in its native habitat allows establishment in immature juniper, hawthorn and beech seres (Watt 1934, Watt 1987a). It is considered a late successional species in sand dune communities in Britain and Western Europe. However, it can be most abundant in pioneer to mid seral communities at newly disturbed sites (Harper and Wood 1957). Tansy ragwort is often found inhabiting poorly managed pastures, recently logged forest, road edges and railroad right-of-ways (Sharrow et al. 1988).

Tansy ragwort is found on many soil types including light sands, loams, clay, and alluvial deposits; but generally most common on lighter, well-drained soils (Harper 1958, Bain 1991). It tends to avoid areas with a high water table or areas with acidic soil (Harper and Wood 1957, Harris et al. 1971, Schmidl 1972, van der Meijden 1974). Soils in tansy ragwort's native range have a pH ranging from 3.95 to 8.2 (Harper and Wood 1957).

Tansy ragwort is found in areas with high annual rainfall in Australia, New Zealand, and historically in North America, (Schmidl 1972, Barkley 1978, Wardle 1987). However, tansy ragwort can now be found in the drier eastern portion of the Pacific Northwest (Burrill et al. 1994) including eastern Washington, eastern Oregon, Idaho and Montana. Tansy ragwort is found in areas of 58 - 130 cm of rain per year in England, and areas exceeding 40 - 51 cm of annual precipitation in the Pacific Northwest of North America (Harper 1958, Coombs et al. 1999). In Oregon, small infestations have been found in areas with only 30 - 35 cm of rain per year (Hawkes 1981). In my study area the fifty year mean annual precipitation is 63 cm, but a substantial proportion of the precipitation is in the form of snow, which is difference from the more commonly inhabited maritime regions.

The first objective of this project was to determine which anthropogenic and environmental variables are correlated with tansy ragwort occurrence and then to create a predictive model of its probability of occurrence. The model can be used to form management recommendations for monitoring of tansy ragwort by identifying areas with high probability of tansy ragwort occurrence which may have higher invasiveness. Another objective of this study was to identify habitat defining variables that correlate with the presence of tansy ragwort in my study area.

Many management areas are too large to conduct a full inventory of non-indigenous species (NIS). However, key element of an effective management approach is the knowledge gained through inventory and survey of the occurrence of NIS (Carpenter et al. 2002). Knowledge of the distribution of NIS enables management prioritization (Carpenter et al. 2002). Knowledge of what environments are currently invaded as well as the extent of the environments vulnerable to future invasions will help predict the potential range of a NIS (Despain et al. 2001) like tansy ragwort.

The modeling project was conducted within the Little Wolf drainage to develop a probability of occurrence map for tansy ragwort, because tansy ragwort is a species of high concern to the landholders within the drainage. Landholders include the United State Forest Service, Plum Creek Timber Company, and the State of Montana. The size of the Little Wolf drainage prevented a full inventory of tansy ragwort in the drainage. Therefore, a stratified random survey method was chosen to sample , create a predictive model and project the occurrence of tansy ragwort.

Materials and Methods

Site Description

The study area was located in the Little Wolf Creek drainage about 120 km southeast of Libby in the northwest corner of Montana. The remote drainage was mostly burned by the Little Wolf wildfire of 1994. Following the wildfire some burned areas were salvage-logged with 90 to 95 % of the salvage-logging completed within two years following the wildfire (Friedman, personal communication, December 5, 2005). The field site used for this study was expanded to include areas outside of the area affected by the 1994 Little Wolf wildfire, but still within the Little Wolf drainage. A total of 4.15 ha within the drainage were surveyed for tansy ragwort occurrence.

Transect Selection

Survey transects for both the summer of 2004 and summer of 2005 were randomly identified but stratified on the main road using digital orthoquads of the study area and ArcView 3.2 geographic information software (GIS). Transects were stratified to be perpendicular to a main road starting on the road but ending at least the length of the transects away from any part of the main (used) road. The transects did intersect other unused roads. Stratification of transects was based on past results that suggested distance from roads accounted for a significant proportion of the variation in NIS occurrence (Gelbard and Belnap 2003, Trombulak and Frissell 2000, Rew et al. 2005).

Twenty transects were established in 2004, each five meters wide by 1000 m long. Another 18 transects were sampled in 2005 and were either 500, 1000, 1500, or 2000 m long. One transect from the summer of 2005 started at the end of a transect from 2004, ultimately resulting in a 2000 m long transect surveyed over the course of two summers. The length of 2005 transects were designed to bisect areas not surveyed in 2004.

Data Collection

Transect data collection and analyses were performed following the methods outlined in Rew et al. (2005). During the 2004 and 2005 field season, the 5 meters wide transects were surveyed on foot by one person for the presence of tansy ragwort, using a Global Position System (GPS). Trimble GeoExplorer 3, Trimble XT and Trimble XM GPS receivers were used to record into a data dictionary the location of each tansy ragwort patch encountered along each transect. The coordinate system and projection used through the length of the project was Universal Transverse Mercator (UTM) Zone 12N, WGS 1984 Datum.

The location of each tansy ragwort patch, the percent cover, the length and width of the tansy ragwort patch was recorded along with habitat type at that location, aspect, and the presence of any disturbance at the location were recorded into the GPS data dictionary. The locations of changes in habitat type and disturbance such as skid trials, rights of way, and game trails were also recorded regardless of whether tansy ragwort was present.

Data Analysis

Using Pathfinder 3.0 Software the data collected were differentially post processed to improve the positional accuracy of the recorded points. The corrected data from both 2004 and 2005 were exported into the GIS, and were converted into continuous NIS data through a series of GIS extensions and an Excel XP macro created by Rew et al. (2005). The result was created continuous presence / absence data for tansy ragwort at 30 m intervals along each transect.

Digital elevation maps (DEM, 30 m resolution) were used to generate specific environmental data layers including aspect, elevation, and slope (degree) at 30 m resolution for the entire study area. The recorded values for aspect were converted to sine and cosine of the azimuth of aspect to identify east / west and north / south components, respectively. Using a road layer that was digitized from a digital orthoquad the distance from the main road was calculated in the GIS. LANDSAT ETM+ (Enhanced Thematic Mapper Plus) remote sensing data for bands one through seven, acquired in July 7, 2001, July 10, 2002, and September 12, 2002 were also included as independent data layers. LANDSAT ETM+ band 6 senses thermal (heat) infrared radiation with a 60 m resolution that is resampled to 30 m. However, because of the diffuse nature of thermal infrared radiation and its subsequent problem with resolution, band 6 is often not used for remote sensing projects. Since we did not have a 1994 Little Wolf wildfire boundary layer, band 6 was included in our project as an independent variable because it effectively delineated the boundary of the wildfire.

Logistic regression was used to estimate the probability of occurrence of tansy ragwort as a function of the independent variables (Menard 1995).

$$P(y=1 \mid x_j) = \frac{\exp(\beta_0 + \beta_1 x_1 + \ldots \beta_i x_j)}{1 + \exp(\beta_0 + \beta_1 x_1 + \ldots \beta_i x_j)} \qquad \text{Eq. 2.1}$$

where y = 1 is the presence of tansy ragwort and x_j are the independent variables included in the logistic regression model for predicting presence. The analysis was preformed in S-PLUS 2000 using generalized linear regression models (GLM), with binomial distribution and logit link (see Rew et al. 2005 for more detail). Akaike's Information Criterion (AIC) (Akaike 1977) was used to determine which independent variables to retain in the model using stepwise procedure for "best" prediction tansy ragwort presence. In addition, the Cp criterion (process capability) statistic was used as an indicator of the relative contribution of each independent variable to the best model. These modeling methods were shown with use of validation data to produce accurate predictions of NIS occurrence in Yellowstone National Park (Rew et al. 2005).

The probability of occurrence map of tansy ragwort was generated by using the best fit GLM regression coefficient values applied to each continuous spatial variable in rasterized format using an extension in the GIS (Rew et al. 2005). In this manner a complete map of the Little Wolf drainage with the probability of occurrence of tansy ragwort was constructed by applying the correlated variables using a raster resolution of 30 m by 30 m (pixels).

In addition to a probably of occurrence map using environmental and remote sensing data we also generated a model using solely the environmental data. We termed this the habitat model, it was constructed using the five independent variables of distance from the main road (first 1000 m), elevation, slope (degree), cosine of aspect (north / south), and sine of aspect (east / west). As above, the habitat model analyzed using logistic regression and the best model selected using AIC and Cp.

Concern about unnecessary retention of independent variables in the best model due to spatial autocorrelation because of continuous transects prompted calculation of Pearson’s correlation coefficients (R 2.1.1) between independent variables which supported dropping some variables (Guisan and Zimmerman 2000, Legendre 1993). Furthermore, a Kolmogorov-Smirnov Goodness-of-Fit Test was used to test for normality of the difference between the distribution of the slope (degree) and the tansy ragwort distribution using Minitab 14.0. If the difference distribution was determined to be non-normal then there was reason to believe that tansy ragwort was more common on some slope angles than others in the sampled areas. The same method was used for determining whether tansy ragwort was more commonly observed on some aspects and at distances from the main road.

Results

Data and Analysis

The transects sampled 4.15 ha of the 8,125 ha study area or 0.051 % (Figure 1.2). A total of 133 occurrences of tansy ragwort were recorded. Following the concatenation of collected data into occurrence at 30 meter intervals, the combination of the data contained 91 occurrences of tansy ragwort and 1333 absences.

Model

The occurrence of tansy ragwort was correlated with most of the environmental variables and remote sense bands tested (Table 2.1). The importance of band 6 in the best model as indicated by the Cp value suggests the importance of the wildfire extent and the predicted occurrence of tansy ragwort. Additionally, distance from the main road and the north / south component of aspect (cosine aspect) were important in the best model. Models with high Cp values have smaller residual deviance.

The probability of tansy ragwort occurrence maps indicates where tansy ragwort is most likely to be present and where it is most likely to be found in the future. A high probability of occurrence based on this model only means that the environmental parameters and reflectance parameters are highly correlated with occurrence and a causative relationship should not be concluded (Figure 2.1). The high probability of occurrence areas were mostly within the boundary of the 1994 Little Wolf wildfire.

Table 2.1. Independent variables used in the best regression model (GLM selected with AIC = 557.87). Variables ordered with descending Cp statistic values[*].

Independent Variables	Coefficient Value	Cp Value
Band 6[c]	0.0716	1128.120
Distance from Main Road	-0.0013	1124.901
Cosine of Aspect	0.8694	1120.832
Band 6[b]	-0.0794	1120.658
Band 2[b]	0.2697	1119.742
Band 7[b]	0.0846	1117.928
Band 1[a]	-0.1707	1116.792
Band 1[c]	-0.1417	1116.313
Band 3[b]	-0.1696	1114.762
Band 7[a]	0.0419	1113.287
Band 4[c]	-0.0251	1113.246
Slope	0.0475	1112.519

[*] Models with a smaller residual deviance have variables with a larger Cp statistic value.
[a] LANDSAT ETM+ 07/07/2001
[b] LANDSAT ETM+ 07/10/2002
[c] LANDSAT ETM+ 09/12/2002

The predicted values of the presence of tansy ragwort were queried to determine the predicted number of hectares at each level of probability (Table 2.2). Tansy ragwort had a mean probability of occurrence in the Little Wolf drainage of 0.032 ± 0.064. Most of the study area had a low probability (0.00 – 0.10) of tansy ragwort occurrence.

Table 2.2. The number of hectares with predicted probability of tansy ragwort occurrence (Study Area = 8125 ha).

Probability	Hectares	Percent of Study Area (%)
0.00 - 0.10	7366.32	90.66
0.10 – 0.20	488.88	6.02
0.20 – 0.40	235.44	2.90
0.40 – 0.60	31.14	0.38
0.60 – 0.999	3.60	< 0.01

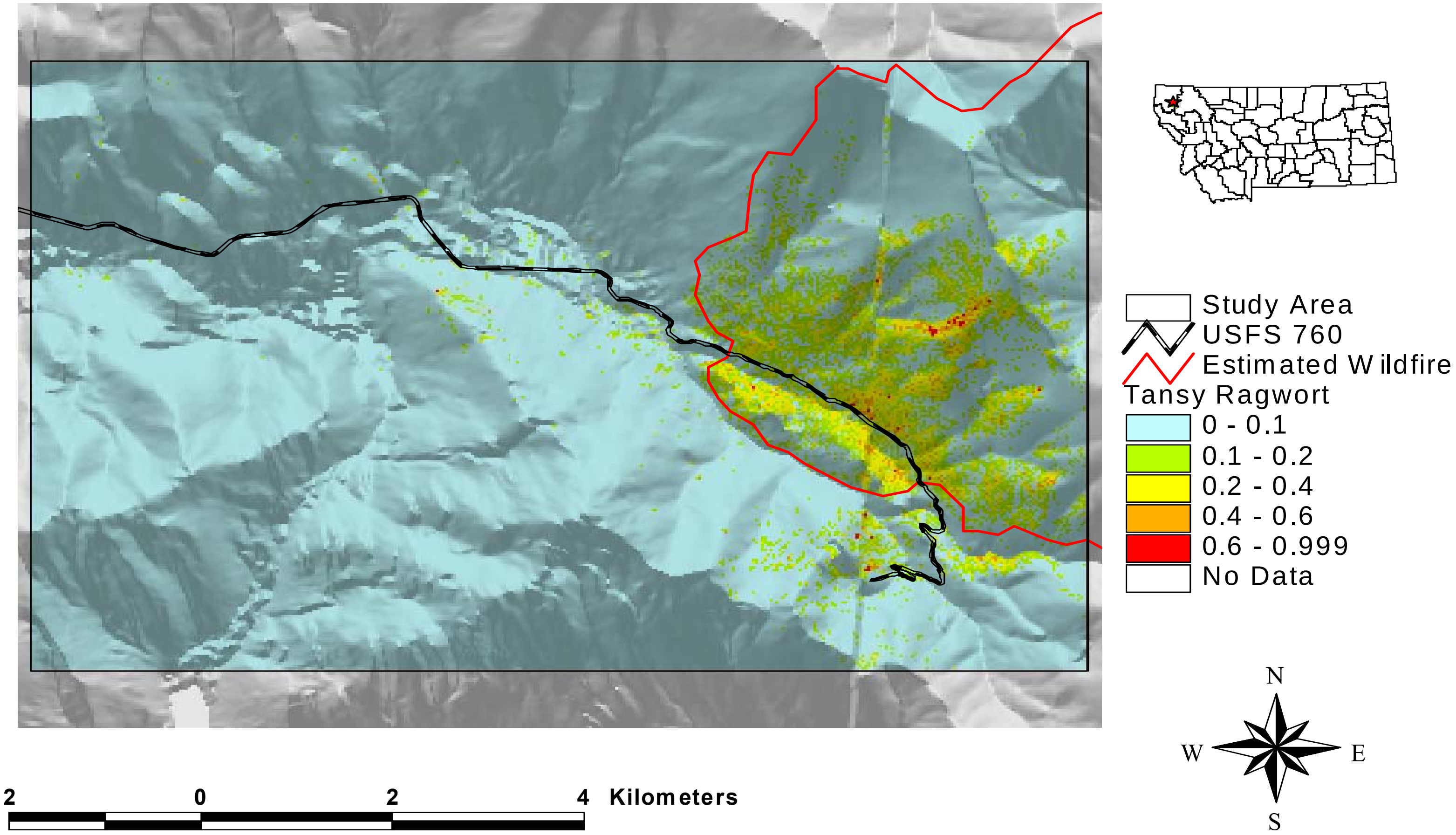


Figure 2.1. Tansy ragwort probability of occurrence map constructed from the data collected during the summers of 2004 and 2005.

Using only the environmental parameters the occurrence of tansy ragwort was correlated with three of the environmental variables, sine of aspect, slope, and distance from road (Table 2.3). Autocorrelation was reduced by removing elevation (elevation and distance from main road, $r = -0.400$; elevation and sine of aspect, $r = 0.414$) and cosine of aspect (cosine and sine of aspect, $r = -0.473$). The east / west component of aspect, the slope, and distance from the main road were important in the best model. Models with high Cp values have smaller residual deviance.

Table 2.3. Independent variables used in the GLM selected with AIC (644.33). Variables ordered with descending Cp statistic values*.

Independent Variables	Coefficient Value	Cp Value
Sine of Aspect	-0.8807	1320.335
Slope	0.0798	1315.300
Distance from Main Road	-0.0009	1312.471

*Models with a smaller residual deviance have variables with a larger Cp statistic value.

Sine of the aspect was a significant variable in the GLM selected with the best AIC for the tansy ragwort habitat model. The regression coefficient value indicated a decreasing presence of tansy ragwort with increasing sine of the aspect, which indicates it being more common on west facing slopes (Table 2.3). The results of the Kolmogorov-Smirnov Goodness-of-Fit test (K.S. = 0.069, $P < 0.010$) indicated that the distribution of the sine of aspect at locations with tansy ragwort was different than the distribution for all recorded sine of aspects. Thus, one could conclude that tansy ragwort is more common on some aspects than others. Using a circular frequency diagram (frequency distribution) with untransformed aspects from locations with tansy ragwort suggested that tansy ragwort has a higher probability of occurrence on west to southwest aspects and some on northeast aspects (Figure

2.2), although the regression analysis indicated that the northeast occurrences were not significant in determining the distribution.

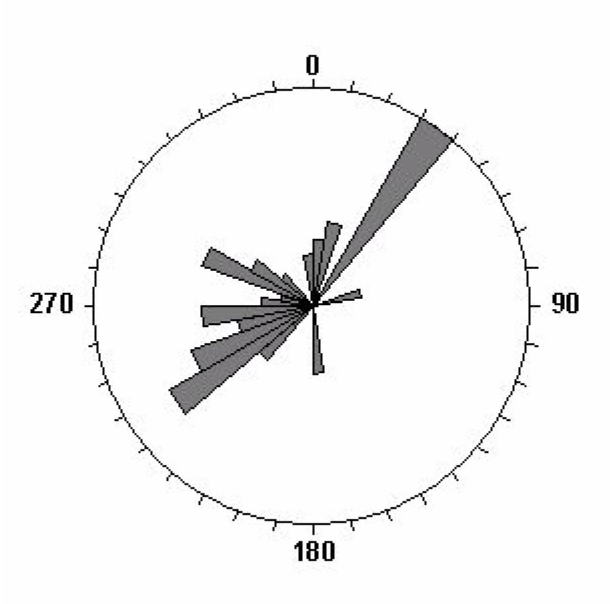


Figure 2.2. Circular frequency diagram of the observed tansy ragwort occurrences by aspect (n = 91) as a proportion of sum of presence and absence (n = 1424).

Slope was a significant variable in the best tansy ragwort habitat model. The regression coefficient value indicated an increasing presence of tansy ragwort with increasing slope (Table 2.3). The results of the Kolmogorov-Smirnov Goodness-of-Fit test (K.S. = 0.015, P < 0.010) indicated the distribution of the slope at locations with tansy ragwort was different than the distribution for all recorded slopes. Thus, tansy ragwort is more common

on certain slope angles. However, the histogram of the distribution of the slopes from locations with tansy ragwort suggests that tansy ragwort has a higher probability of occurrence with increasing slopes up to 13 or 14 degrees and becoming nearly absent with higher slopes (Figure 2.3).

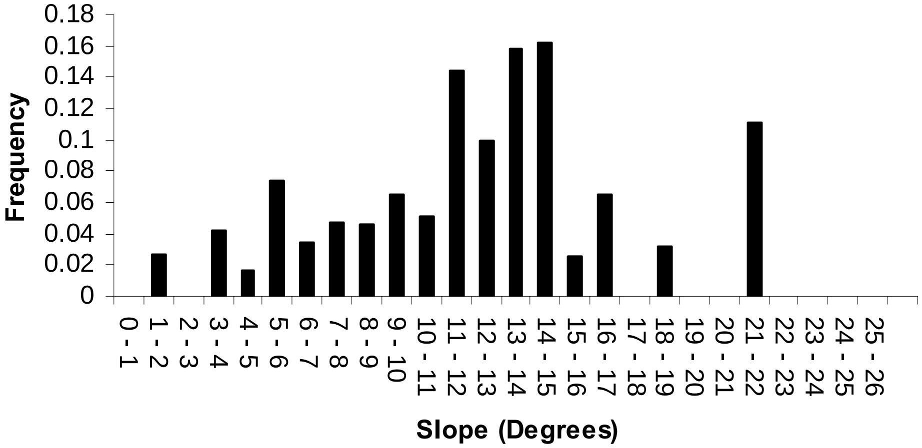


Figure 2.3. The slope of tansy ragwort occurrence (n = 91) as a proportion of sum of presence and absence (n = 1424). Angel the x axis at 90 degrees.

Distance from the main road was also a significant variable used in the tansy ragwort presence best habitat model. The regression coefficient value for distance from main road was negative, indicating a decline in the presence of tansy ragwort with increasing distance from the main road (Table 2.3). The results of the Kolmogorov-Smirnov Goodness-of-Fit test (K.S. = 0.045, P < 0.010) indicated the distribution of the distance at locations with tansy ragwort was different than the distribution for all recorded distances. Therefore, tansy ragwort has a higher probability of occurrence at areas closer to the main road. The histogram of the distribution of the distance from the main road for locations with tansy ragwort indicates that tansy ragwort increased in frequency for the first 300 meters away from the road and had a decreasing frequency as distance from the road increased beyond 300 meters (Figure 2.4).

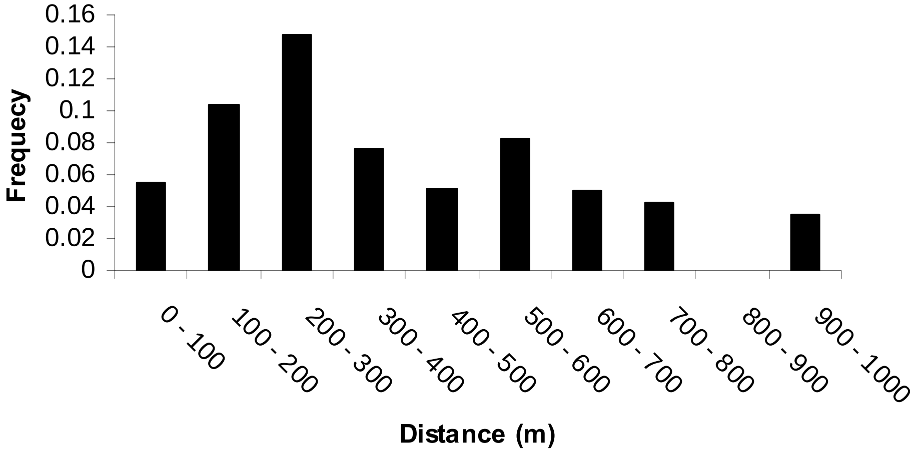


Figure 2.4. The distance from main road of tansy ragwort occurrence (n = 79) for first 1000 m of transect as a proportion of sum of presence and absence (n = 1218).

Discussion

The applied significance of our findings include that land managers efforts to locate new populations of tansy ragwort can be directed to the indicated areas with high probability of tansy ragwort occurrence while areas with low probability can be given a lower priority. In addition, different levels of probability of occurrence can be used to stratify population selection for monitoring to determine relative invasiveness and impact on management objectives.

LANDSAT ETM+ band 6 was used as a surrogate to define the extent of the wildfire because there was no GIS wildfire boundary layer. The predictive map showed that areas within the boundary of the 1994 Little Wolf wildfire have the greatest probability of tansy ragwort occurrence. This relationship is supported by the literature showing that disturbance plays a role in the presence of tansy ragwort as a pioneer to mid seral species at newly disturbed sites (Harper and Wood 1957). The wildfire disturbance should decline due to regeneration of vegetation as time from the wildfire increases (Larson and Franklin 2005), and as the habitat recovers and the cover of other species increases tansy ragwort may not establish or compete well (Watt 1987b). Conversely, if tansy ragwort is well established before the habitat recovers from the wildfire disturbance, tansy ragwort may compete with surrounding vegetation (McEvoy 1984a).

The regression coefficient in the probability of occurrence model indicated that tansy ragwort occurrence decreased as distance from the main road increased. Distance from roads has been investigated and suggested as a significant factor influencing NIS presence (Timmins and Williams 1991, Trombulak and Frissell 2000, Weaver et al. 2001, Gelbard and Belnap 2003, Rew et al. 2005). Over the length of the sampled transects, distance from the main road showed a negative trend with tansy ragwort occurrence. However, a positive trend was identified for the occurrence of tansy ragwort for the first three hundred meters from the roadway. This may indicate a confounding effect of active roadside spraying which could reduce tansy ragwort density near the roadside. Additionally, dispersal of populations away from roadways could account for increased occurrence of tansy ragwort for the first three hundred meters from the roadway. Higher frequency of presence was also recorded at 500 to 600 m and again at 900 to 1000 m away from the main road. The higher frequency might indicate locations of minor roads and trails not used in constructing the distance from road variable.

Management Implications

Many management areas are too large to fully sample for occurrence of NIS. Sampling without bias identifies the environmental conditions correlated with NIS occurrence. However, if the survey for NIS is conducted early in the invasion, this method might miss all possible environments that could be invaded.

Using the correlated environmental conditions to construct a predictive map can assist in prioritizing locations to monitor for new and existing populations and to monitor existing populations for variability in invasiveness and impact on management objectives. Even without the generation of predictive maps, the knowledge of how environmental variables relate to NIS distribution can help managers prioritize where to manage for NIS under the preliminary assumption that the correlated environmental variables function as determinates of occurrence of the NIS. Once the survey for the occurrence of NIS is complete, management can focus on monitoring NIS for invasiveness (Chapter 3), the impact of NIS occurrences and the impact of NIS management (Chapter 6).

CHAPTER 3

ESTIMATING POPULATION GROWTH RATES USING DEMOGRAPHIC MODELS TO PRIORITIZE MANAGEMENT OF TANSY RAGWORT

Introduction

Non-indigenous species (NIS) are increasingly becoming an important concern to conservation, as it has been reported that NIS can be a threat to native community structure (Simberloff 1981) and ecosystems (Mack et al. 2000). Even though many studies have been conducted concerning NIS, we are still unable to predict the attributes and conditions that enable a species to be invasive (Mack et al. 2000). Understanding population dynamics and variability across environments during invasion could be particularly important for improving the efficiency of NIS management.

The toxicity of tansy ragwort (*Senecio jacobaea* L.) to livestock and some wildlife has made this species a concern for land managers (Deinzer et al. 1977, Goeger et al. 1981). The presence of tansy ragwort has caused loss of grazing land due to its toxicity (Goeger et al. 1981, Isaacson and Ehrensing 1977). Tansy ragwort is classified as a noxious weed in Arizona, British Columbia, California, Colorado, Idaho, Montana, Nova Scotia, Oregon, and Washington (Rice 2005), and is native to Europe and Asia (Harper and Wood 1957, Jeffrey and Chen 1984). Before 1991 populations of tansy ragwort were observed only in maritime regions of North America but populations moved inland in the 1990s and now can be found in the northwest corner of Montana (Rice 2005). In Montana, tansy ragwort was classified as a noxious weed following the colonization of areas in the northwestern region of the state that were burned in a 1994 wildfire (Richardson 1997).

Models of plant population dynamics are increasingly being used to target vulnerabilities and to predict the impact of management methods, including biological control organisms, on the abundance of target NIS (Maxwell et al., 1988, Shea and Kelly 1998, McEvoy and Coombs 2000, Allendorf and Lundquist 2003). A model of the population biology of a species might help identify the density or spatial extent at which a goal of containment rather than eradication should be pursued (Allendorf and Lundquist 2003).

Models have been used to investigate hypotheses, formulate theory and prioritize management. With a field parameterized model of leafy spurge population (*Euphorbia esula* L.), Maxwell et al. (1988) used sensitivity analysis to demonstrate that transition rates from the basal buds to vegetative shoots, survival of vegetative shoots, and the over winter survival of basal buds were influencing population growth. The model was also used to simulate control strategies that were compared to population response with field studies to correlate model and field results (Maxwell et al. 1988).

A matrix model constructed by Shea and Kelly (1998) tested the impact of biological control and other management strategies on nodding thistle (*Carduus nutans* L.) in New Zealand. Shea and Kelly (1998) were able to confirm that the nodding thistle populations were increasing at two areas with their single species, stage-structured matrix model. In addition, they showed that the seed to seedling and small plant to seed transition rates were most important to the population growth with elasticity analysis.

Our research goal was to quantify the variation of tansy ragwort population growth rate (λ_{env}) under several environmental conditions in northwest Montana. In our investigation of the invasiveness of tansy ragwort, we are using the definition that an invasive species is a NIS that is consistently increasing in density and / or spatial extent. A designation of invasive under this definition does not imply impact on the ecosystem or management goals (Rejmánek et al. 2002).

Population invasibility analysis (PIA) was started in 2001 with the construction of a life history model for tansy ragwort parameterized for populations found in several different environments. These environmental designations offered conditions to examine the variability of the tansy ragwort λ. If variability in λ was found to correspond to the different environments it would allow management prioritization of the tansy ragwort populations.

The PIA was based on a series of difference equations parameterized with field data collected from the spring of 2001 to the fall of 2005. The null hypothesis was that tansy ragwort λ would not differ between environmental conditions. The alternative hypothesis was that λ would be greater than 1.0, fitting our definition of invasive and the degree that it was greater than 1.0 would serve to prioritize populations for management.

Identifying the most important transition rates to population growth can improve the ability to target management practices. Therefore, a secondary objective of the field study was to determine the transition that contributed the most to the λ of tansy ragwort in the study area. The null hypothesis was that all transitions would equally contribute to the λ of tansy ragwort. The alternative hypothesis was that not all transitions would equally contribute to the λ and knowing which stages contribute proportionally the most to growth rate would serve to target management.

Materials and Methods

Area Description

The study areas were located in a remote area about 120 km southeast of Libby in the northwest corner of Montana (Figure 1.2). All of the areas were located in the Little Wolf Creek drainage within an area that was mostly burned by the Little Wolf wildfire of 1994. Following the wildfire some burned areas were salvage-logged with 90 to 95 % of the salvage-logging completed within two years following the wildfire (Friedman, personal communication, December 5, 2005).

Areas were identified in June of 2001 that had a south to southwest facing slopes and using Pfister et al. (1977) definition a forest to grassland vegetation habitat types. In 2001 populations of tansy ragwort were identified in four environments including: 1) areas burned by the Little Wolf wildfire of 1994, 2) areas burned by the wildfire and then salvage-logged, 3) non-burned forest, and 4) non-burned meadow. In 2004 the four environments were reevaluated and the non-burned forest was redefined as a burned environment because the area was so small (an island in the burn) and the forest canopy trees were dying as a result of fire damage and had begun to fall over. As a result the under story environment was not distinguishable from the burned areas. Therefore in 2004 the study environments were established as: 1) areas burned by the Little Wolf wildfire of 1994, 2) areas burned and then salvage-logged, and 3) non-burned meadow. Within these three environments, four study areas were identified in the burned and salvage-logged environment, five areas in burned with no salvage-logging, and one small area of non-burned meadow. Due to the extent of the area burned by the 1994 fire, only one non-burned meadow area was located that contained tansy ragwort populations. One of the ten study areas was located on private land owned by Plum Creek Timber Company and the remainder were on the Kootenai National Forest. Physical characteristics in addition to distance to nearest biological control release area, and topographic position of all of the 10 study areas are summarized in Table 3.1.

From 2000 to 2005 the mean annual precipitation for the study area of the Kootenai National Forest was 41.91 cm. For the same period the mean annual temperature was 4.52 °C, the mean annual minimum temperature was -3.24 °C, and the mean annual maximum temperature was 12.22 °C (Table 3.2, Appendix E).

The soils in the study area are Andic Dystric Eutrochrepts, fine-silty, mixed, frigid loam (Kuennen and Nielsen-Gerhardt 1995). The area burned by the wildfire has been closed to grazing since the Little Wolf fire of 1994.

Population invasibility analysis (PIA) was performed using ten 1.0 m^2 plots at each area except for the meadow environment where only five plots were established due to the small tansy ragwort infestation. Each plot was considered to be an individual population of tansy ragwort. Populations were located by Trainor (2003) using an adaptive sampling method to ensure that an unbiased estimate of λ could be made for each environment (Thompson 2002). A 100 m baseline transect was established by roughly bisecting the selected environment where tansy ragwort was observed (Trainor 2003). For the burned and salvage-logged and burned environment transect, the 1 m^2 plots were established by traveling the baseline transect a random distance then heading perpendicular to the baseline at a random direction a distance until a tansy ragwort plant was encountered (Trainor 2003).

Where as at the meadow area, plots were established at all five patches of tansy ragwort located in that environment (Trainor 2003).

Table 3.1. Selected environmental characteristics for all of the ten study areas in the Kootenai National Forest.

Environment[a]	Biological control release area[b] (km)	Elevation (m)	Aspect	Slope (degrees)	Mean Percent Sky (%)[c]	Habitat type[d]
BSL	1.61	1183	S-SW	14	48.1 (19.81)	ABLA/ CLUN
BSL	1.61	1229	SW	16	53.3 (21.83)	PICO/CARU
BSL	2.25	1480	S-SW	7	32.9 (5.63)	ABGR/XETE
BSL	0.4	1702	S-SW	12-15	70.0 (16.76)	ABGR/XETE
Burned	1.61	1218	SW	5	49.0 (12.45)	ABGR/ CLUN
Burned	1.61	1225	SW	5	53.6 (14.67)	PICO/CARU
Burned	2.25	1475	S-SW	20	47.9 (15.12)	PICO/LIBO
Burned	3.22	1680	S	2-5	47.8 (21.36)	ABLA/ CACA, GATR phase
Burned	0.16	1705	SW	24	66.1 (21.52)	ABGR/XETE
Meadow	2.41	1224	S-SW	3	47.1 (12.56)	FEID/DECE

[a] BSL = burned and salvage-logged.

[b] Distance to nearest insect biological control agent release area.

[c] Mean (± standard deviation) Percent Sky from LAI – 2000 Plant Canopy Analyzer, LI – COR = fraction of sky that is not blocked by foliage.

[d] ABLA, *Abies lasiocarpa*; CLUN, *Clintonia uniflora*; PICO, *Pinus contorta*; CARU, *Calamagrostis rubescens*; ABGR, *Abies grandis*; XETE, *Xerophyllum tenax*; LIBO, *Linnaea borealis*; CACA, *Calamagrostis canadensis*; GATR, *Galium triflorum*; FEID, *Festuca idahoensis*; DECE; *Deschampsia cespitosa* (for habitat type description, see Pfister et al. 1977).

The plots were censused for tansy ragwort plants in late May / early June and August

2001 through 2005 by overlaying a 1 m^2 frame with a 1 / 16 m^2 grid to record location and life-cycle stage of the each tansy ragwort plant. Sampling from 2001 through 2003 was conducted by Trainor (2003).

Table 3.2. 2000 through 2005 total annual and 50 year annual mean (± standard deviation) precipitation (cm) and mean (± standard deviation), mean minimum (± standard deviation), and mean maximum (± standard deviation) temperatures (°C) from the Libby 32 SSE, Montana weather station near the study area.

	2000	2001	2002	2003	2004	2005	50 Year
Mean Precipitation	40.1	44.1	57.8	47.7	49.4	46.1	61.1 (14.07)
Mean Temperature	4.0 (8.04)	4.7 (7.77)	4.3 (7.59)	5.1 (8.52)	5.4 (7.33)	4.4 (8.36)	4.7 (8.97)
Minimum Temperature	-4.2 (5.51)	-3.5 (5.25)	-3.0 (5.93)	-3.0 (5.93)	-1.9 (5.66)	-3.4 (6.95)	-2.4 (5.90)
Maximum Temperature	12.2 (10.70)	12.9 (10.59)	11.6 (9.60)	13.1 (11.23)	12.7 (9.16)	12.3 (10.18)	12.0 (9.92)

Transition Rates

Recording individual tansy ragwort plants within each 1 m^2 plot enabled us to follow the fate of each plant and calculate life history transition rates twice per year (Figure 3.1) with the difference equation approach or with a Lefkovitch transition matrix approach using transition rates calculated from the fall census data each year (Appendix D). The Lefkovitch matrix model served as validation for the more detailed difference equation approach and was used to streamline the process of estimating the λ and elasticity analysis. Thus, a secondary objective of this study was to determine whether the two-census-per-year difference equation approach added useful information over the single census matrix approach.

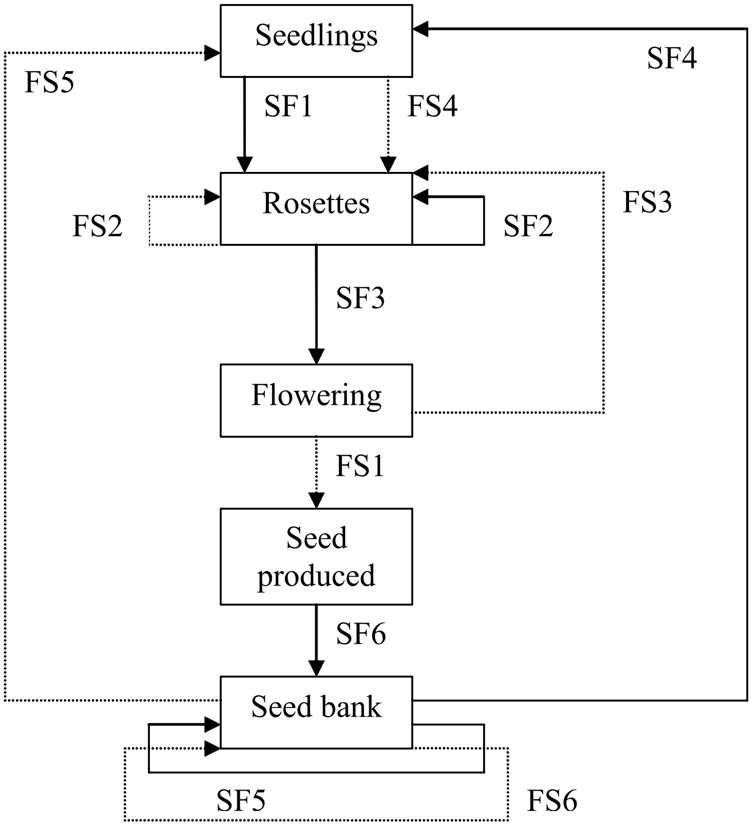


Figure 3.1. Life-cycle model for tansy ragwort with two transition rates recorded per year. The life history stages (states) are in squares and the arrows indicate calculated transition rates. Solid arrows labeled SF indicate spring-to-fall transition rates; dashed arrows labeled FS indicate fall-to-spring transition rates.

The population transition rates have been measured twice per summer since the spring of 2001. This enabled the construction of a model using two transition rates, a spring-to-fall and a fall-to-spring (Table 3.3). The matrix elements, SF (spring-to-fall) and FS (fall-to-spring) define the transition rate from time *t* - 1 to time *t*. The transition rates other than reproduction are proportions that vary from 0 to 1. An individual can remain in a particular stage, move up at least one stage, or even revert to an earlier life stage.

Table 3.3. Two transition rate matrices of a stage-structured life-cycle model of tansy ragwort with the use of two transitions per year. Matrix elements (SF = spring-to-fall transition rate; FS = fall-to-spring transition rate) represent the probabilities that individuals in one size class year $t-1$ (columns) will enter a class year t (rows). Zeros indicate transition rates that do not exist or were not calculated in this study. For values see Table D.6.

	Seedling	Rosette	Flowering	Seed Produced[a]	Seed Bank[b]
Seedling	0	0	0	0	SF4
Rosette	SF1	SF2	0	0	0
Flowering	0	SF3	0	0	0
Seed Produced	0	0	0	0	0
Seed Bank	0	0	0	SF6	SF5
	Seedling	Rosette	Flowering	Seed Produced[a]	Seed Bank[b]
Seedling	0	0	0	0	FS5
Rosette	FS4	FS2	FS3	0	0
Flowering	0	0	0	0	0
Seed Produced	0	0	FS1	0	0
Seed Bank	0	0	0	0	FS6

[a] The probability for seed produced to enter the seed bank (SF6) was set to 1.0 because we assumed immigration was equal to emigration.

[b] The probability for seed to remain in the seed bank was set to each area's respective seed survival rate as found from the seed burial study explained in the text.

In order to calculate the transition rates, plants were grouped into classes that included seed bank, seed production, seedlings, rosettes, and flowering plants. The seed bank was estimated from seed production and seed survival rate, seedlings were defined as having five leaves or less, rosettes had six or more leaves or a plant with five leaves or less present for two consecutive censuses, and flowering plants contained a bolted stem with flowers.

At the first census performed in the spring of 2001, each tansy ragwort plant location was mapped on graph paper corresponding to the 1 / 16 m^2 grid overlaying the plot. Further censuses were conducted using acetate paper overlaid on the pervious census map. Overlaying the maps allowed individual plants, to be tracked and transition rates to be calculated. Seedlings that survived to the next census became rosettes. Rosettes that appeared where a flowering plant had been the previous census were considered to be vegetatively reproduced unless cotyledons were observed.

Transition rates for the life history model with two transitions per year were calculated following a set of rules (Table 3.4).

Table 3.4. Explanation of the calculation of tansy ragwort transition rates for the life history model using two transitions per year.

Transition	Calculation	Where:
SF1	sdltorossf = ros_{fallt}/ $sdl_{springt-1}$	sdltorossf = number of seedlings that transitioned to rosettes from the spring census to the fall census, sdl = number of seedlings, ros = number of rosettes, t = current time (year)
SF2	rostorossf = ros_{fallt}/ $ros_{springt-1}$	rostorossf = number of rosettes that remained rosettes from the spring census to the fall census
SF3	rostoflwsf = flw_{fallt}/ ros $_{springt-1}$	rostoflwsf = number of rosettes that transitioned to flowering shoots from the spring census to the fall census, flw = number of flowering plants
SF4	sbtosdlsf = seedlings $_{fall\ t}$ / (seed $produced_{fallt-1}$ * mean seed survival $rate_{environmental\ type}$);	sbtosdlsf = number of seedlings transitioning from seeds after accounting for the survival of the seed bank, sb = number of seeds in seed bank
SF5	sbtosbsf = mean seed survival $rate_{environmental\ type}$	sbtosbsf = mean (standard deviation) seed bank survival rate for each environmental type
SF6	sptosbsf = 1	sptosbsf = number of seeds produced that reach the seed bank, estimated as 1 (migration = emigration), sp = number of seeds produced
FS1	flwtospfs = estimate of seed production	flwtospfs = estimate of seed production based on the number of flowering plants / plot
FS2	rostorosfs = $ros_{springt}$/ $rostorossf_{fallt-1}$	rostorosfs = number of rosettes that remained rosettes from the fall census to the spring census
FS3	flwtorosfs = $ros_{springt}$/ $flw_{fallt-1}$	flwtorosfs = number of flowering plants that reverted to rosettes from the fall census to the spring census
FS4	sdltorosfs = $ros_{springt}$/ $sdl_{fallt-1}$	sdltorosfs = number of seedlings that transitioned to rosettes from the fall census to the spring census (over winter).
FS5	sbtosdlfs = $seedlings_{spring\ t}$ / (seed $produced_{fallt-1}$ * mean seed survival $rate_{environmental\ type}$)	sbtosdlfs = number of seedlings transitioning from seeds after accounting for the survival of the seed bank
FS6	sbtosbfs = mean seed survival $rate_{environmental\ type}$	sbtosbfs = mean (standard deviation) seed bank survival rate for each environmental type

Transition rates were calculated for each 1 m^2 plot and then the median transition rate was calculated from all populations within each environment type. The median values for specific transition rates were qualitatively compared between the three environmental types using a box and whisker plot that included the median, the 95 % confidence intervals for the median, 50 % of the data, and outliers for the transition rates.

Seed Production

The transition rate from flowering shoots to seed production (FS1) was estimated by randomly selecting flowering plants in each environment at the time of the fall census (August). All of the selected flowering plants were outside of the monitored populations. The randomly selected plants were clipped, their capitula counted, and a sample of seed per capitula were counted to estimate mean seed produced per flowering plant.

Seed Bank

To quantify the seed survival rate in the soil seed bank, tansy ragwort seeds were buried in ten areas representing the three different environments by Trainor (2003). The viability of the seeds was tested in 2001 prior to burial and in 2002, 2004, and 2005. In October 2001 six fine mesh nylon bags containing seed were buried 2 cm below the soil surface at each area along the baseline transect. Each of the bags contained 200 seeds. Two bags were unearthed at each area in August of 2002 (Trainor 2003), 2004, and 2005; except at the meadow environment and at one burned environment where only two bags were unearthed in 2002 and none the following years due to failure to relocate the bags.

The seeds from the nylon bags were counted. If less than 200 seeds were counted, it was assumed that the missing seeds were the results of decay, germination without emergence, or predation. In addition to the buried seeds, a sample from the original seeds was kept in a laboratory drawer since 2001 to determine the base decay rate and viability. Viability of these seeds was tested in August of 2002, 2004, and 2005. To test the seeds from the field and stored seeds for germination and viability we followed a method outlined in Baskin and Baskin (1998). Seeds were placed onto blotting paper moistened with distilled water and incubated at 19 ^{o}C for 30 days. Additional distilled water was added when needed to ensure the blotting paper remained moist. Seeds were examined visually every two days for germination. Germination was determined by the presence of the emerged hypocotyl. After 30 days, non-germinated seeds were tested for viability. Additionally, a second set of seeds from the unearthed buried seeds that had not been tested for germination was tested for viability. These seeds served to control for any loss of seed viability during the germination test.

To test the non-germinated seeds for viability, the seeds were placed on moist blotting paper over night to imbibe. Seeds were classified as dead when no solid material was present within the seed coat (Baskin and Baskin 1998). Once imbibed, each seed was nicked with a razor blade and placed in a Petri dish with 1 % tetrazolium solution overnight at 19 ^{o}C. The treated seeds were examined the following morning with a microscope for color change. Tetrazolium causes in a red color change in viable embryos when it reacts with dehydrogenase (Simpson 1990). Thus, seeds with red stained embryos were considered viable and those that were patchily stained red or remained white were considered non-viable. Therefore, the seeds that had not germinated within the 30 day germination test, but remained viable, were then considered dormant (Baskin and Baskin 1998). The decay rate of the buried seeds was calculated from the relationship between the viability of the unearthed seed samples and time of burial.

Population Growth Rate

We used λ as a measure of tansy ragwort population invasion potential. That is, the higher the λ, the higher the invasion potential. In addition, population prioritization for management could be conducted based on the relative invasiveness (prob. $\lambda > 1.0$) of populations in each environment.

The initial population vectors were represented by the fall 2001 mean values of seeds, seedlings, rosettes, flowering plants, seed productions, and seed bank for each of the environments. The previous work conducted by Trainor (2003) using the same study areas found that the initial population did not affect λ distributions. The initial population vectors (initial population size) were multiplied by the fall-to-spring transition rates to obtain the modeled spring population vector. The spring population vector was then multiplied by the fall-to-spring transition rates to produce the following fall population vector.

The difference equation method modeled the λ for each plot. Each sample population was simulated for 20 generations with Monte Carlo resampling of sets of transition rates from different years associated with the plot (population). The λ for a given environment was calculated based on the changes of rosettes plus flowering shoot density in the fall for the final two generations ($\lambda = \text{density}_t / \text{density}_{t-1}$) of a simulation. The population dynamics were simulated for 20 generations to ensure that the simulated population had reached a stable stage distribution. A stable stage distribution was defined as the generation when the proportion of plants in each stage was consistent from generation to generation. A distribution of the λs was accumulated for each environment type by repeating the simulation of population dynamics 1000 times per environment, each time selecting a set of transition rate values from a randomly selected plot and time step within an environment.

Standard statistical comparison between the estimated λ of each environment was impossible due to high and non-normally distributed variability. Instead, we used a bootstrap technique to calculate the probability of the populations from an environment exceeding a λ greater than 1.0, where any λ greater than 1.0 met the minimum criteria for being invasive. This approach to analysis provided the best fit to our ultimate objective of prioritizing populations for management based on the environments where they were found.

Elasticity Analysis

Values of elasticity indicate the relative impact of each transition rate on the λ (Caswell 1989). Elasticity analysis was used to determine which transition rates were proportionally most important to regulation of tansy ragwort population density. This was achieved by investigating the proportional change in population density when mean transition rate parameter values were individually changed by a constant proportion and thus could be targeted by management. Elasticity analysis values were calculated as:

$$\text{Elasticity values} = \left(\frac{parameter}{\lambda}\right)\left(\frac{\Delta\lambda}{\Delta parameter}\right) \text{ (Caswell 1996),} \qquad \text{Eq. 3.1}$$

where parameter and λ were the original (default) parameter and resultant λ values and Δ parameter and Δ λ were the change in parameter and resultant growth rate values from the original. Elasticity analysis was defined in this study as the proportional change in density of mature plants (rosettes plus flowering plants) in the fall due to a proportional (10 % reduction) adjustment to the transition rate values. Elasticity's were measured after twenty generations and were reported as a proportional importance relative to the parameter having the greatest impact.

Lefkovitch Matrix Model

A Lefkovitch matrix model based on the transition rates for one transition per year served as validation for the difference equation method. This method reduces the number of field observations by almost one half and thus, if found to provide similar answers to the more detailed difference equation approach, could streamline the process of estimating λ and elasticity values (Appendix A). The Lefkovitch matrix model reduced the field census time to one time per year, and both the math to estimate λ and the elasticity analysis. The transition rates used in the Lefkovitch included the same transition rates calculated from the fall census each year (Appendix A).

The λ for each population was calculated with the Lefkovitch matrix model using seed bank values from successive years. Two simulations methods with the Lefkovitch were tested. The first method selected transition rates within each plot randomly for each year of the simulation. The second method selected transition rates within each plot in order of year recorded for the first five generations and then randomly selected transition rates within the same plot for each of the remaining years of the simulation. The dominant eigenvalue of the Lefkovitch matrix was the λ. A Monte Carlo simulation was used to create a distribution of the estimated λs using observed variation in the transition values from 20 simulation runs per plot.

Statistical Analysis

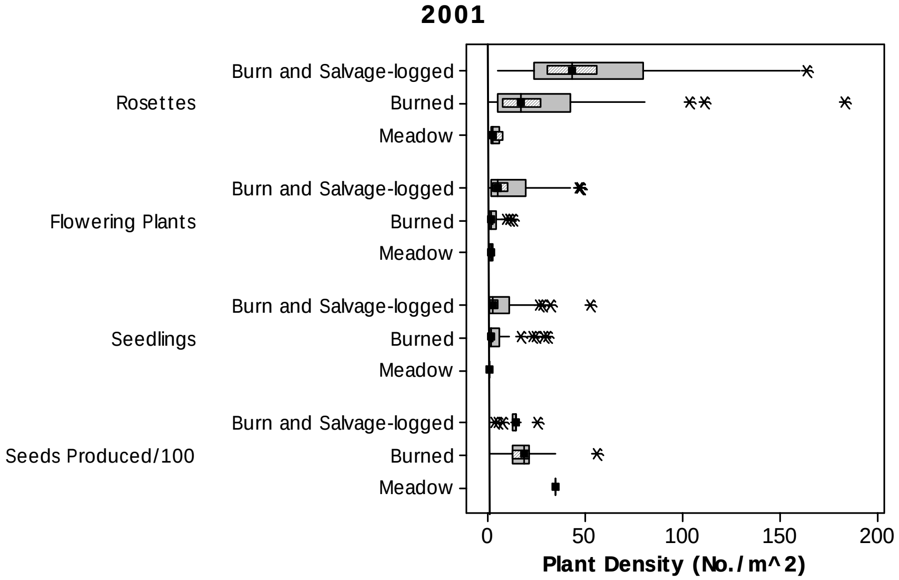
Statistical analyses were performed with Minitab 14.1, S-Plus 2000, R 2.1.1, and Excel XP. Median transition rates for the three environments were compared qualitatively using box and whisker plots that were created with Minitab 14.1. The box and whisker plots included 95 % confidence intervals for the median. Therefore, if the median confidence intervals for two boxes did not overlap, the two parameter values were considered to be different with 95 % confidence.

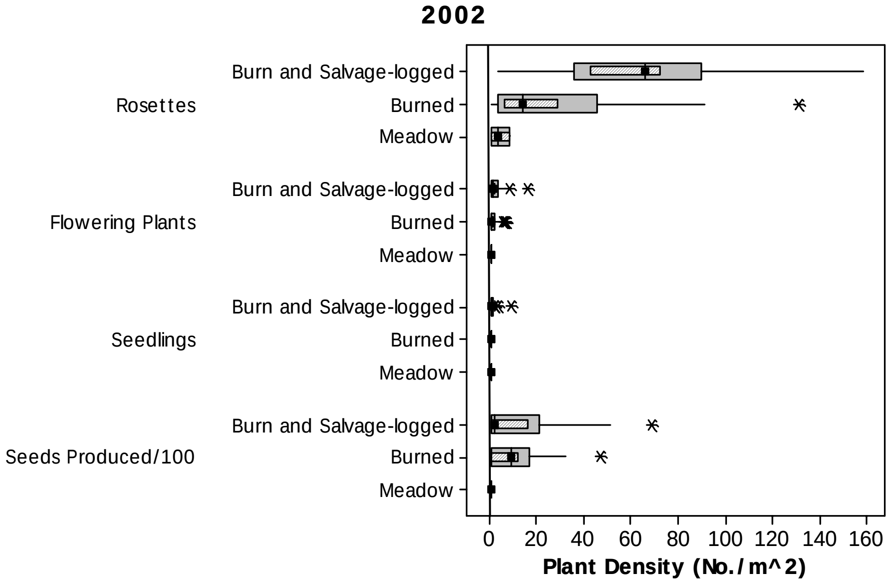
The λs for the model simulations using difference equations and the validation model were tested for significant differences using box and whisker plots generated with Minitab 14.1. Like the comparison of transition rates, the box and whisker plots of the λs included 95 % confidence intervals for the median. Additionally, the probability for each environment of λ greater than 1.0 (defined as invasive) was calculated as the proportion of the simulated iterations resulting in a λ greater than 1.0. The model calculations and elasticity analysis for the difference equation approach were performed in Excel XP with programs and population analysis macros programmed by Bruce Maxwell while the Lefkovitch matrix method used for validation and elasticity analysis was conducted in R.2.1.1 (programs available in Appendix B, C)

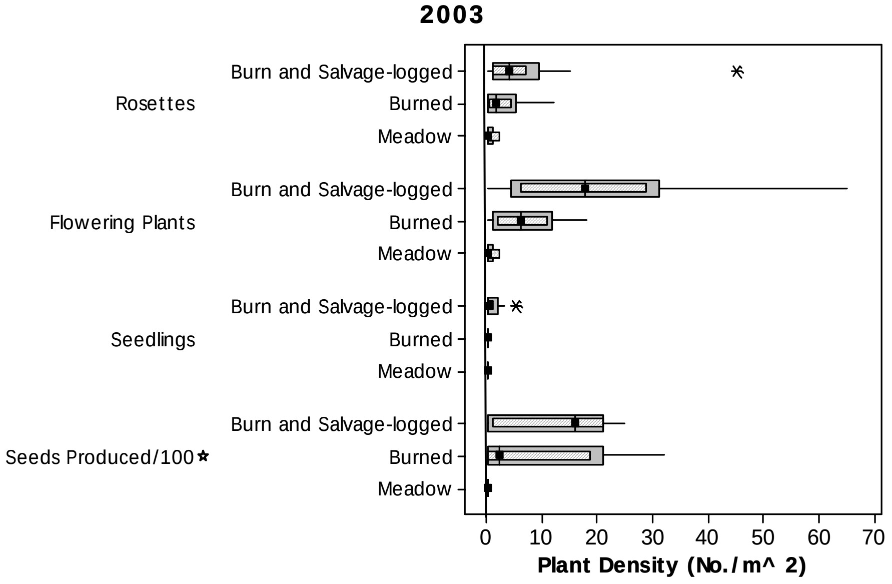
Results

Transition Rates

Individuals were counted and their life history stage noted from plots in three different environments (burned and salvage-logged, burned, and meadow) to quantify the transition rates of the tansy ragwort populations. The distributions of density (plants / m^2) of individuals in each life-stage were similar across years (2001 to 2005) (Figure 3.2 and Table 3.5). However, 2003 had lower numbers of rosettes than the other three years. Additionally, the distribution for 2003 was proportionally similar to that of the other four years of data, but the values were greatly reduced. Seed production data for 2003 was based on the number of seeds per plant from 2002, because seed production data was not collected in 2003.







*Seed production for 2003 based on number of seeds per flowering plant from 2002.

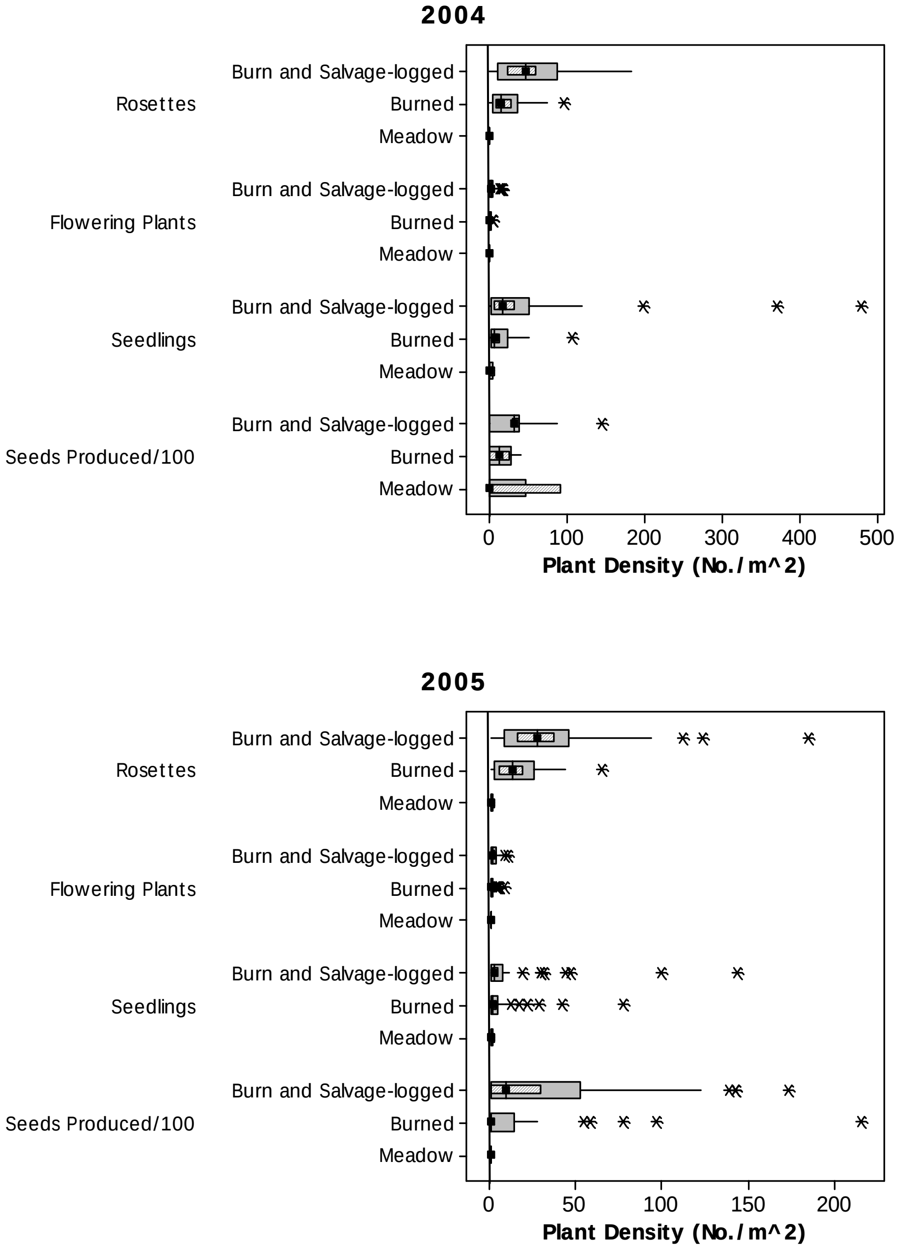


Figure 3.2. Plant density of tansy ragwort individuals in each life-history stage for fall 2001, n = 95 (A), fall 2002, n = 95 (B), fall 2003, n = 45 (C), fall 2004, n = 94 (D), and fall 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (horizontal lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different. Seed production values were divided by 100 so that all four stages could be represented in the same figure.

Table 3.5. Mean number of rosettes (± standard deviation) and flowering plants (standard deviation) per 1 m^2 in the three different environments. The 2003 data was based on two burned areas, two burned and salvage-logged areas, and the meadow area.

	Fall 2001		Fall 2002		Fall 2003		Fall 2004		Fall 2005	
Area	Rosettes	Flowering	Rosettes	Flowering	Rosettes	Flowering	Rosettes	Flowering	Rosettes	Flowering
Burned and Salvage-logged	64 (48)	5 (6)	60 (46)	2 (3)	21 (20)	1 (1)	53 (46)	3 (4)	37 (39)	2 (3)
Burned	29 (36)	2 (3)	26 (29)	1 (2)	7 (5)	0 (1)	23 (23)	1 (1)	16 (15)	1 (2)
Meadow	3 (2)	1 (1)	4 (4)	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)

The distribution of the mean number of capitula per flowering plant was similar across the burned and salvage-logged and burned environments from 2001 through 2005. The meadow environment did not produce any flowering plants within the populations from 2002 through 2005 (Figure 3.3).

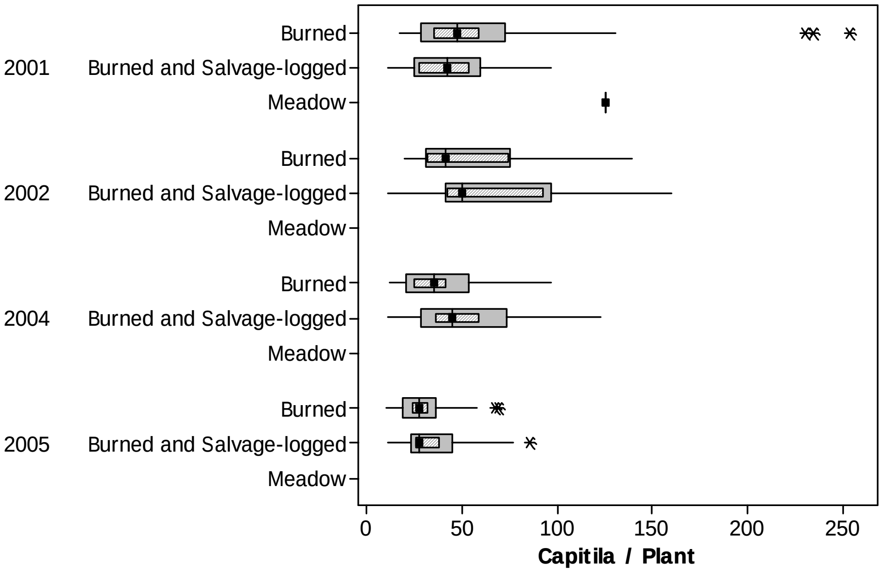


Figure 3.3. Number of capitula for flowering plants from each environment fall 2001, n = 95 (A), fall 2002, n = 95, (B), fall 2004, n = 94 (C), and fall 2005, n = 94 (D). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (horizontal lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

The means and standard deviations of the number of capitula per plant were used in the estimation of the mean seed production per environment. The distribution of the estimated seed production was similar for the burned and salvage-logged and burned environments from 2001 to 2005 (Figure 3.4).

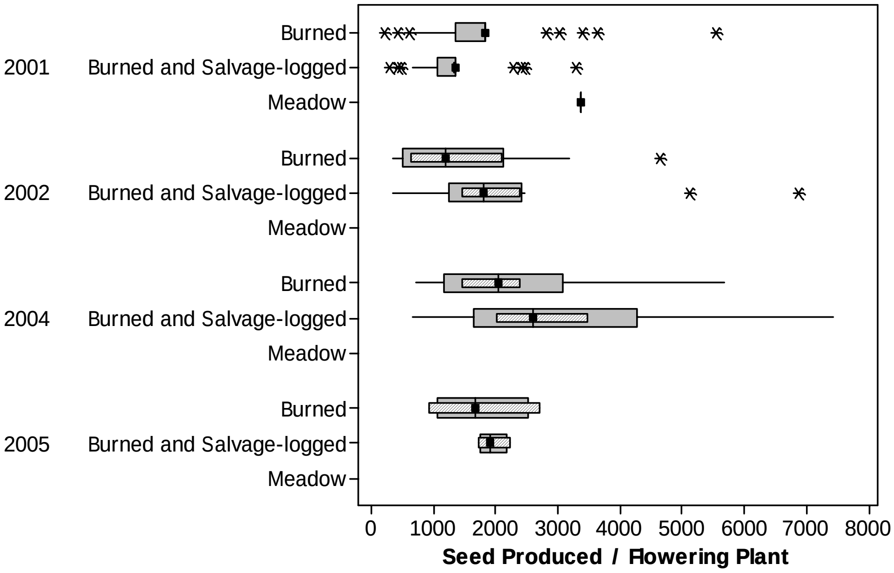


Figure 3.4. Number of seed produced per flowering plant from each environment fall 2001, n = 95, fall 2002, n = 95, fall 2004, n = 94, and fall 2005, n = 94. Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (horizontal lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

Seed Bank

The seeds used for the seed burial experiment were 82 % viable before burial in the summer of 2001. Table 3.6 shows the viability of stored and buried seed after one year (10 months), three years, and four years. Trainor (2003) found that the seed buried in the forest and meadow areas had the highest mean percent viability (Table 3.6 and Figure 3.6); while the seed buried in the burned area had the lowest mean percent viability after ten months. However, Trainor (2003) reported that there were no statistical differences in seed viability after 10 months, except between the burned and the meadow environments ($P > 0.0441$, d.f. = 9) and between the burned and the seed viability preburial ($P > 0.04$, d.f. = 9) (Table 3.6 and Figure 3.5).

Table 3.6. Mean percentage viability over time (± standard deviation) of stored seed and of seed buried at 2 cm in three different environments. No seed collected 2003.

		Mean viable seed			
Year	Time (years)	Stored (%)	Burned and Salvage-logged (%)	Burned (%)	Meadow (%)
2001	0	82	82	82	82
2002	1	75	57 (19.3)	37 (19.5) [a,b]	70 (9.5)[a]
2004	3	65 (14.1)	42 (24.2) [b]	34 (34.2)	-
2005	4	48 (38.9) [a]	0 (0) [a,b]	23 (31.9) [b]	-

[a] Comparison significant at $\alpha = 0.05$ within each year.

[b] Comparison significant at $\alpha = 0.05$ with preburial viability.

Figure 3.5. Mean seed survival by years after burial by environment. No seed collected 2003.

No seed bank samples were tested in after two years of burial (2003). The meadow area was not located after three years of burial and the forest area was reclassified as a burn area in 2004. After three years there was no significant differences in seed viability among the environments, except between the burn and salvage-logged and the seed viability before burial (P = 0.036, d.f. = 16). After four years of burial the significant differences in seed viability among the environments were between burn and salvage-logged and laboratory stored (P = 0.048, d.f. = 4), between burn and preburial (P = 0.033, d.f. = 9) and between burn and salvage-logged and preburial (P = 0.000, d.f. = 4) (Table 3.6).

Seed buried in the burned environment lost viability more rapidly than seed in the other environments for the first year of burial, however, the burn and salvage-logged environment was the first to lose all viability. This indicated that the seed bank in the most heavily disturbed area might not contribute to the population dynamics without regular input from seed rain. The dried seed stored in the laboratory lost viability slower than any of the environments. The measurement of seed bank viability was used to estimate the seed bank decay rate or the five years (Table 3.7).

Table 3.7. Seed bank decay rate with 95 % confidence intervals.

Environment	Decay Rate	95 % Confidence Interval
Burned and Salvage-logged	0.74	± 0.161
Burned	0.82	± 0.277
Meadow	0.88	*
Laboratory Storage	0.89	± 0.193

*Decay rate based on preburial and sample after one year.

Comparing Mean and Median Transition Rates

Mean transition rate values were calculated from the transition rates from 2001 through 2005 for each of the three environments (Table 3.8).

Table 3.8. Mean (± standard deviation) for each transition rate from 2001 through 2005. (See Appendix D for mean (standard deviation for each transition rate for each year)

	Mean transition rate values(2001-2005)[a]										
Areas[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.59	0.78	0.07	0.01	0.72	1724	0.61	0.08	0.29	0.04	0.72
n = 40	(0.388)	(0.241)	(0.125)	(0.043)	(0.142)	(1975)	(0.273)	(0.211)	(0.352)	(0.330)	(0.142)
B	0.52	0.74	0.09	< 0.00	0.72	1103	0.65	0.02	0.23	0.01	0.72
n = 50	(0.459)	(0.723)	(0.182)	(0.011)	(0.720)	(1372)	(0.366)	(0.114)	(0.388)	(0.021)	(0.720)
M	0.20	0.56	0.05	0.00	0.88 ([c])	1271	0.37	0.00	0.00	0.00	0.88 ([c])
n = 5	(0.345)	(0.557)	(0.129)	(0.000)		(2676)	(0.409)	(0.000)	(0.000)	(0.001)	

[a] see Table 3.2 for definition of transition rates

[b] BSL = Burned and Salvaged-logged, B = Burned, and M = Meadow; n = number of plots (1 m^2) used to calculate mean

[c] Decay rate based on two sampling periods

We found the transition rates were highly variable and non-normally distributed. Transition rates varied by environment, in distribution, in shape of distribution (non-normal), and in central tendency (median). Therefore, box and whisker plots were used to qualitatively assess differences between environments, by enabling the distribution and central tendency to be visualized. Comparison of transition rates between years and environments showed that the transition rates of tansy ragwort varied little in distribution from 2001 through 2005 with a few exceptions. One of these exceptions was the seedling to rosette transition rate (SF1) from spring-to-fall. This parameter was variable through the length of the project. For both the burned and salvage-logged and the burned environment the seedling to rosette transition rate (SF1) was lower in 2002 than 2001, and then alternated up and down for the remaining years (Figure 3.6).

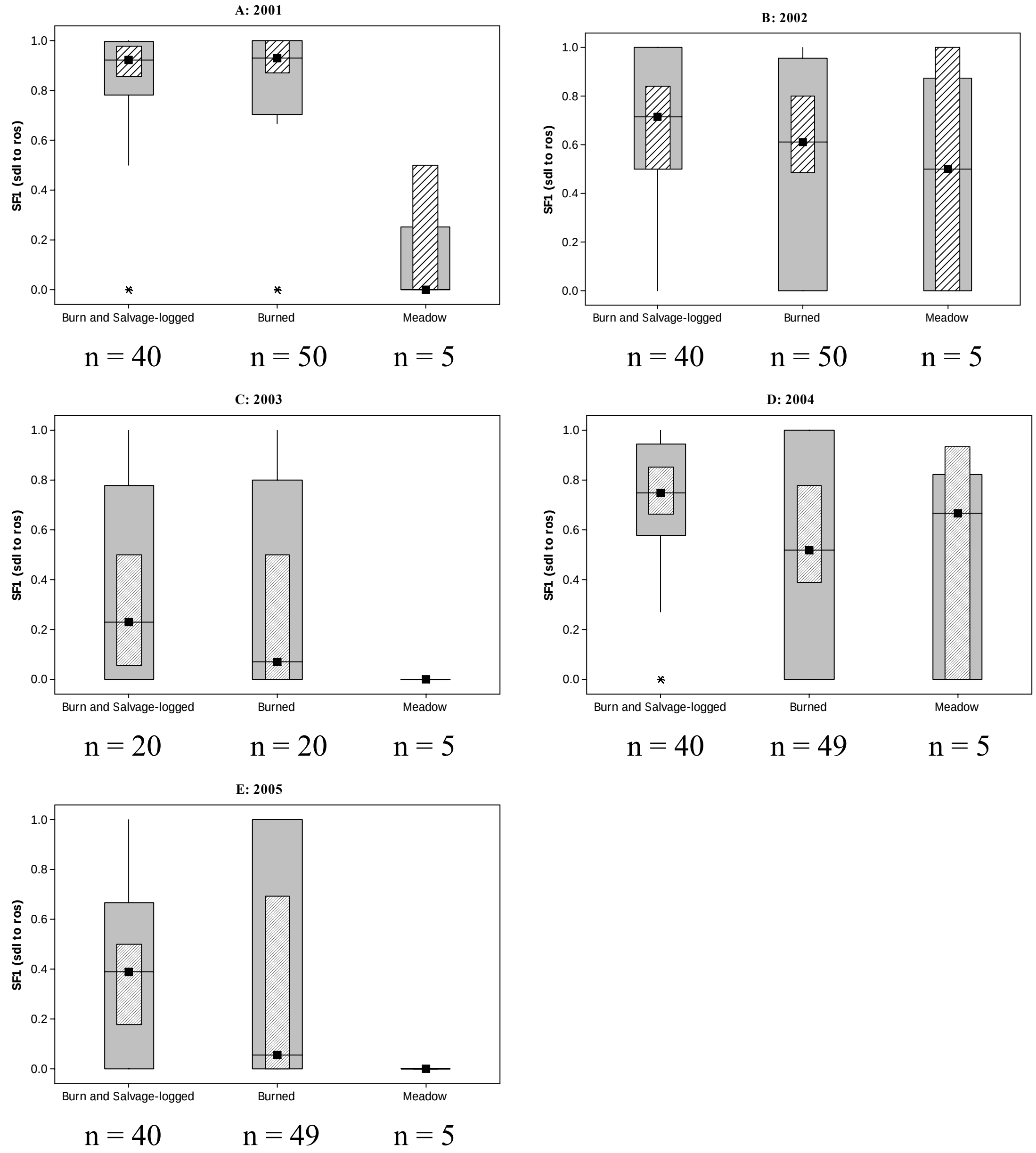


Figure 3.6. Spring-to-fall seedling to rosette transition rate (SF1) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different. See Appendix D for more figures comparing median transition rates for the three environments.

Another transition rate that changed through the period 2001 to 2005 was the rosette to flowering plant transition rate (SF3) for the meadow environment. The meadow environment produced flowers in 2001 but failed to produce any flowers from 2002 through 2005. As a result of no rosette transition into flowering plants (SF3) the flowering to seed production (FS1) for the meadow environment became zero. If one assumes that there is flowering and seed production once every five years in the meadow environment at the rates that we measured in 2001, then the λ would eventually decline if conditions remained constant.

Population Growth Rates

There was high and non-normally distributed variability in estimated λ. However, none of the 95 % confidence levels for λ calculated for the three environments overlap after five years of data indicating a significant difference between environments ($\alpha = 0.05$) (Figure 3.7). A clear prioritization for management could be identified based on the relative invasiveness (prob. $\lambda > 1.0$) of populations growing in each environment. This qualification would allow a more sensitive measure of the population growth (Table 3.9).

Table 3.9. Probability of populations in each environment having a growth rate (λ_{env}) greater than 1.0 using the life-cycle model with two transitions per year and Monte Carlo simulation randomly selecting sets of transition values from different years.

Environment	Probability of $\lambda > 1.0$
Burned and Salvage-logged	0.309
Burned	0.204
Meadow	0.013

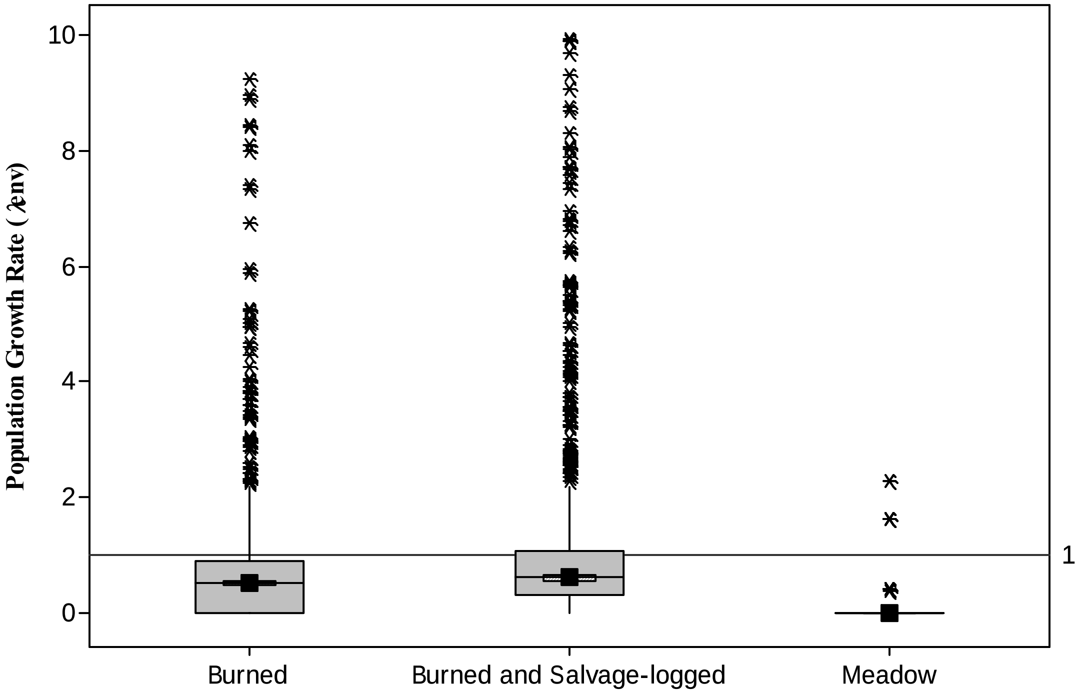


Figure 3.7. The λ of tansy ragwort based on life-cycle model with two transitions per year using the difference equation modeling method. Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. Outliers ranging from 10 – 985 were removed from the box plot for Burned and Salvage-logged and from 10 – 409 for the Burned environments to display the central tendency of the distribution. If the confidence intervals did not overlap, the two responses were judged to be significantly different.

Elasticity Analysis

Elasticity analysis was performed using the mean transition rate values for each environment. Changing these transition rates showed that the over winter and over summer rosette-to-rosette transition rates (FS2 and SF2) and the over winter and over summer transition rate of seed bank to seed bank (FS6 and SF5) were of greatest relative importance in the life cycle of tansy ragwort in each of the three enviroments (Table 3.10).

Table 3.10. Elasticity values (0-100) using mean transition rates (Table 3.4) for each enviroment with a –10 % change in parameter values over 20 generations. Values of 100 are most important.

Transition rate	Burned and Salvage-logged	Burned	Meadow
FS1 (flw to sp)	0.000	0.000	0.000
FS2 (ros to ros)	88.347	74.352	33.804
FS3 (flw to ros)	0.099	0.002	0.000
FS4 (sdl to ros)	0.000	0.000	0.000
FS5 (sb to sdl)	0.000	0.000	0.000
FS6 (sb to sb)	100.000	100.000	100.000
SF1 (sdl to ros)	0.002	0.001	0.000
SF2 (ros to ros)	88.347	74.352	33.804
SF3 (ros to flw)	0.107	0.005	0.000
SF4 (sb to sdl)	0.061	0.009	0.000
SF5 (sb to sb)	100.000	100.000	100.000

The transition rates found to be the most important with elasticity analysis were qualitatively compared among environments with box and whisker plots. Comparison of the box and whisker plots for the over winter and over summer rosette survival (FS2 and SF2) showed no significant difference between environments except that both the over winter and over summer survival of rosettes in the meadow was lower than either the burned or burned and salvage logged environment (Appendix D). The seed bank to seed bank over winter and over summer survival (FS6 and SF5) were not compared across years for they were constant based on the seed bank decay rate for the length of the study.

Emergence rates of seedlings for the model simulations were calculated based on counts of new seedlings as a proportion of the seed produced per plot the previous fall multiplied by the mean seed bank survival rate for each environment (FS4 and SF5, Table 3.3). However, the seed produced per plot used in the emergence calculation were estimates from plants outside of the populations. Therefore, knowing the elasticity of the flowering to seed production transition rate (FS1) and the seedling emergence transition rates (SF4 and

FS5) were important for understanding how plants from outside of the populations would affect the results of the modeled λ. Elasticity values for seedling emergence and the flowering to seed produced transition rates were zero or very low when assessed at 20 generation with a 10 % reduction (Table 3.10). This is consistent with Crawley (1983), which reported that in a mesic grassland that tansy ragwort's growth rate was insensitive to changes in fecundity.

Model Validation: Population Growth Rate

The λ for each environment was estimated using the Lefkovitch stage-structured life-cycle matrix model based on one transition per year (Table 3.11).

Table 3.11. Median of the estimated λ and the probability of λ being greater than one (increasing) based on Monte Carlo simulation.

Environment	Difference Equation[a]		Lefkovitch[b]		Lefkovitch[c]	
	Median λ	Prob. (λ) > 1.0	Median λ	Prob. (λ) > 1.0	Median λ	Prob. (λ) > 1.0
Burned and Salvage-logged	0.683	0.309	0.834	0.256	0.826	0.246
Burned	0.533	0.204	0.818	0.107	0.818	0.119
Meadow	0.000	0.013	0.880	0.000	0.880	0.000

[a] Difference equations based on transition rates from a life-cycle with two transitions per year.

[b] Validation Model: Lefkovitch matrix model based on randomly selected transition rates from a life-cycle with one transition per year.

[c] Validation Model: Lefkovitch matrix model based on consecutive transition rates followed by randomly selected transition rates from a life-cycle with one transition per year.

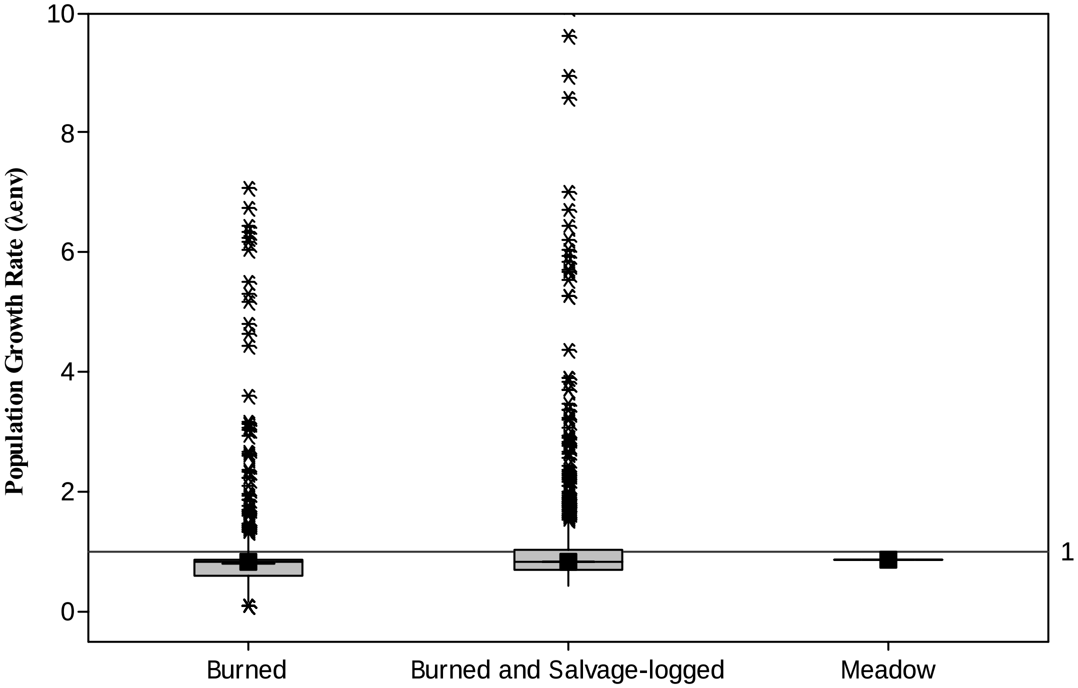


Figure 3.8. The λ of tansy ragwort based on life-cycle model with one transitions per year using the Lefkovitch matrix modeling method (method 2, figure 3.11). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), and 95 % confidence interval for the median (hatched box) across environments. Outliers ranging from 10 – 141 were removed from the box plot for burned and salvage-logged and from 10 – 204 for the burned environments to display the central tendency of the distribution. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

The second Lefkovitch matrix model method (Lefkovitch^c in Table 3.11) was tested to determine if selecting transition rates in chronological order for the observed years would affect the projected λ. Both Lefkovitch methods estimated similar median λs and probability of λ > 1. The burned and salvage-logged environment had a slightly higher median λ and probability of λ > 1 when transition rate were randomly selected for the entire length of the simulation versus selecting transitions in chronological order for the first five years of the simulations. The burned environment had the same median λ and lower probability of λ > 1 when transition rate were randomly selected versus selecting them in chronological order. Due to the estimates being only slightly different, we used the first Lefkovitch method (Lefkovitch[b] in Table 3.11) that selected transition rates within each plot randomly for each year of the simulation because it was more similar to the difference equation approach.

None of the 95 % confidence levels for the three environments overlapped indicating that the λs were found to be different between environments using the Lefkovitch model (Figure 3.8) as was the result with the more detailed difference equation model (Figure 3.7). The models provided consistent probabilities that λ was greater than 1.0 (Table 3.11). Thus, one may conclude that the Lefkovitch model requiring only one set of observations per year was just as effective as the more detailed difference equation model for distinguishing differences in λs and relative invasiveness of populations.

Model Validation: Elasticity Analysis

The Lefkovitch matrix model was used to validate the elasticity values produced with the difference equation approach. The Lefkovitch matrix model elasticity analysis found rosette survival and seed bank survival as the most important transition rates in determining the λ of tansy ragwort for all three of the environments (Table 3.12). Thus, the results with elasticity analysis were consistent between the two models reinforcing the advantage of using the Lefkovitvh model approach.

Table 3.12. Elasticity values (0-100) using mean transition rates (Table A.2) for each enviroment with a -10 % in parameter vlaues over 20 generations. Values of 100 are most important.

Transition rate	Burned and Salvage-logged	Burned	Meadow
T1 (sb to sdl)	8.323	3.032	0.000
T2 (sdl to ros)	8.323	3.032	0.000
T3 (ros to ros)	100.000	100.000	66.667
T4 (flw to ros)	0.963	0.480	0.000
T5 (ros to flw	8.861	3.998	0.000
T6 (flw to sp)	10.127	4.595	0.000
T7 (sp to sb)	9.782	3.032	0.090
T8 (sb to sb)	70.795	98.544	100.000

Discussion

Variability in Invasiveness

Standard statistical comparison between the tansy ragwort λs for each environment was eliminated due to high and non-normally distributed variability in the estimated λs_{env}. Therefore, using the probability that $\lambda_{env} > 1.0$ as a measure of relative invasiveness of the populations in the different environments enables management prioritization of populations by environment. Thus, the burned and salvaged-logged environment with a probability between 0.31 and 0.24 of $\lambda > 1.0$ would be a top priority for populations management followed by the burned environment (prob. $\lambda > 1.0 = 0.20$ to 0.10), and finally the meadow environment where growing populations of tansy ragwort were so rare that management is probably unwarranted. The ranking of environments highlights the importance of disturbance, which may account for the relative population invasiveness.

Our work and Trainor (2003) suggest that populations may have been locally increasing through 2002, but as time from the disturbance event of the 1994 Little Wolf wildfire and subsequent salvage-logging increased, the median growth rate for tansy ragwort decreased. Yet, even 11 years following the wildfire, there were populations with extremely high projected growth rates. This suggests that populations can continue to be invasive given the right conditions, but those conditions become rarer as time since wildfire disturbance increases.

Elasticity Analysis

Elasticity values indicate that the survival of rosettes over winter (FS2) and over summer (SF2) and the seed bank survival rate for each environment (FS4 and SF5) were of greatest relative importance in the life cycle of tansy ragwort in each of the three environments. The finding that the survival of adult tansy ragwort plants was important to the λ was consistent with Prins et al. (1990), in that tansy ragwort plant size before or just after winter was the primary determinant of flowering. Additionally, the importance of seed bank survival supports the conclusions of Thompson and Makepeace (1983) that accelerating seed death was necessary for tansy ragwort control.

Alternative Tansy Ragwort Model

The model using difference equations based on two transitions per year and the validation models using a Lefkovitch matrix based on one transition per year produced similar results for the projected median λ and the probability of populations of tansy ragwort in each environment being locally increasing or invasive. Additionally, the modeling methods found the same ranking of the environments based on median λs. Further, the models produced similar results for the elasticity analysis. These results suggest that future studies could use a Lefkovitch matrix model based on one transition per year to reduce model complexity and data for parameterization. However, the role of seed bank survival seemed to drive the estimates of λ for the meadow environment with the Lefkovitch model more than the difference equation approach, emphasizing that caution should be used, because a model based on one transition per year will reduce the number of parameters, which might result in errors of omission from failing to include important transition rates or interactions in the life-cycle.

Management Implications

As the time from wildfire and salvage-logging disturbance increases and the native vegetation recovers, the λ should continue to decline (Chapter 4). With the exception of the occasionally invasive tansy ragwort populations and without renewed disturbance, these populations appear to be declining to local extinction. Therefore, management should reduce the risk of renewed disturbance by focusing on monitoring to determine whether populations will increase in density and require management, or whether the populations will decline naturally to local extinction.

Populations that are increasing in density and require management should be managed to most effectively impact the λ. Based on the elasticity analysis, the use of management methods including biological control agents that focus on reducing seed production will have little effect on the λs. Rather, the elasticity analysis suggests that management should focus on reducing the survival of rosettes and the seed bank.

Management targeting rosette survival supports the conclusion of Bain (1991) who reported that hormone-like herbicides applied during seedling or rosette stage provided the best chemical control of tansy ragwort. In addition to the use of herbicide, rosette survival can be affected with the use of biological control agents such as the ragwort flea beetle (*Longitarsus jacobaeae* Waterhouse) and the cinnabar moth (*Tyria jacobaeae* L.) (Binns 1976, Prins and Nell 1990). Additionally, we found that with increased native cover tansy ragwort λ and rosette survival declined (Chapter 4).

Seed bank survival is difficult to manage directly; however, previous studies with tansy ragwort have showed that growing vegetation and accumulation of litter can suppress germination of tansy ragwort in the field (Cameron 1935, Meijden and Waals-Kooi 1979, Crawley and Nachapong 1985, McEvoy and Rudd 1993). Therefore, we expect that as more litter is produced and the native vegetation and canopy cover recovers from wildfire and logging, the ability of tansy ragwort to produce seeds that will germinate should diminish. Management that speeds the closure of the canopy cover, such as revegetating with trees at a higher than normal density in areas with tansy ragwort populations, should reduce both the germination rate of tansy ragwort and the rosette survival.

CHAPTER 4

SOURCES OF TANSY RAGWORT POPULATION GROWTH VARIABILTY

Introduction

Knowing how the spatial and temporal availability of resources as well as density dependence affects the variability of population growth rate (λ) of non-indigenous species (NIS) may help managers better prioritize which populations need management. The role of available resources and the establishment of NIS has been debated (Tilman 2004, Stohlgren 2003). Plants need to obtain the required resources for survival from the environment. However, not all individual plants or populations of the same species are the same. Plant species differ in survival and success across gradients of resources, competition for those resources and response to stress (Tilman 1991). Thus, plants evolve different strategies for acquiring resources and surviving stress resulting in their general characterization as ruderal, competitor, or stress-tolerating species (Grime 2001).

Competition for resources can be between individuals of the same species (intra-specific) and between individuals of different species (inter-specific). Density dependence is a result of intraspecific competition and has frequently been observed in plant populations (Buckley et al. 2001). Density dependence has been incorporated into models of plant population (Maxwell et al. 1988) to make stage-classified population dynamics more realistic by influencing specific demographic transition rates (Neubert and Caswell 2000).

Density dependence can be the result of competition for available resources. The resources needed by plants are dispersed heterogeneously within and across environments.

Therefore, local conditions might be more favorable to the establishment and growth of one population of a species than another. Spatial heterogeneity of resources levels could explain the variation in λ of populations of the same species across environments. The addition of temporal heterogeneity of the resource supply in the environment or time from a disturbance event can further explain the variability in λ.

The objective of this study was to identify sources of variability of the tansy ragwort (*Senecio jacobaea* L.) λ and demographics (e.g. transitions between life history states, seed production and vegetative reproduction) within and across environments in a northwest Montana study area. This objective was potentially addressed using population dynamics modeling described in Chapter 3. Starting in 2001, the λ of tansy ragwort was estimated across several broad environments including: 1) areas burned by the Little Wolf wildfire of 1994, 2) areas burned by the wildfire and then salvage-logged, 3) non-burned forest, and 4) non-burned meadow (Trainor 2003). In 2004 the non-burned forest was determined to be a replicate of the burned environment type because trees initially thought to be an unburned island in the larger wildfire began to die from injury sustained during the fire. These broad environmental designations enabled estimation of tansy ragwort λ across factors that might contribute to variability in the λ. The null hypothesis was that density dependence and environmental variables would not contribute to the variability of the tansy ragwort λ in the study area. The alternative hypothesis was that density dependence and environmental variables would contribute to the variability of λ within and across environments where tansy ragwort has become established.

Material and Methods

The study area was previously described in Chapter 3. The field areas were located 120 km southeast of Libby, Montana. All of the sites were within the area burned by the Little Wolf wildfire of 1994. Following the 1994 wildfire some burned sites were salvaged-logged with 90 to 95 % of the salvage-logging completed within two years following the wildfire (Friedman, personal communication, December 5, 2005).

Population Growth Rate and Important Transition Rates

The λs were calculated for each of the three environments from transition models parameterized using data collected from 2001 to 2005 from 5 to 50 populations (plots) in each environment (Chapter 3). The influence of intra- and inter-specific density or abundance, and environmental factors on λ and specific demographic transitions following the measurement of the independent variables was investigated. Specific demographic transitions were identified as proportionally important to the λ using elasticity analysis (Caswell 2001). The proportionally most important transition rates included the over winter and over summer rosette survival (FS2 and SF2) and the over winter and over summer seed bank survival (FS6 and SF5). However, the over winter and over summer seed bank survival (FS6 and SF6) was not included in the analysis because those rates were calculated from a limited number of observations mostly made in the first 2 years of the study.

Density Dependence

Linear regression was used to investigate intra-specific density dependence as a relationship between λ (t_n) and density of mature plants (rosettes + flowering plants) (t_{n-1}) (Chapter 3). Intra-specific density dependence was also investigated in the relationship of over winter and over summer rosette survival (FS2 and SF2) (t_n) as a function of density of mature plants (t_{n-1}). Intra-specific density dependence was investigated using linear regression and ocular estimates of the percent cover of species other than tansy ragwort within the plots. Percent cover was estimated in fall of 2001, 2002, and 2004. Relationships were investigated for percent cover (t_{n-1}) and tansy ragwort λ and the over winter and over summer rosette survival (FS2 and SF2) (t_n). The regression analyses tested the hypothesis that a significant negative slope would be detected and thus conclude that density dependence was operating.

A combination of inter- and intra-specific density dependence was investigated with an end of growing season measurement of the fraction of sky that was not blocked by intra- plus inter-specific foliage. This measurement will be referred to as percent sky, with values that ranged from 0 (no sky visible to the sensor) to 1 (no foliage visible to the sensor) (LI – COR 1992). The percent sky measurement was taken during the fall 2004 census for each plot using a LAI – 2000 Plant Canopy Analyzer, LI – COR. The 2005 transition rates and the tansy ragwort λ were hypothesized to increase with the percent sky using linear regression analysis.

Environmental Variables

The relationship of specific environmental variables and the most important transition rates as determined with elasticity analysis was investigated with linear regression. These included the over winter and over summer rosette survival (FS2 and SF2).

Trainor (2003) collected soil samples in May of 2002 at eight of the ten study transects. Soil was collected to a depth of 10 cm adjacent to each of the 1 m^2 plots for a total of 85 soil samples. The soil samples were dried at 49 ^{o}C for 48 hours, then ground using a mortar and pestle and sieved to remove coarse fragments. The samples were sent to be analyzed at MDS Pharma Services, Inc. (Lincoln, Nebraska) to determine total N, percent organic matter (OM), pH, particle size, cation exchange capacity (CEC), and major nutrients (P, K, Mg, and Ca). Data for Olsen P (P) and Exchange K (K) were tested against the significant transition rates (FS2 and SF2) calculated from 2001 to 2002 data. Total N (N), determined by the Kjeldahl determination method; percent OM; pH; and CEC were tested for their influence on the same transition rates from the length of the study because these independent variables were thought to have less temporal variability (Jones, Montana State University, November 12, 2005).

Precipitation data were collected from the Western Regional Climate Center. The mean annual precipitation for the year previous to the recording of the transition rates and the mean annual precipitation for year of the transition rates were used as independent variables to identify relationships with the transition rates over the length of the study. Additionally, transition rates were tested as a function of the year the transition rate was collected. Using the year the transition rate was collected as an independent variable allowed identification of trends in the transition rates as time from the wildfire increased.

Statistical Analysis

Tests for density dependence and environmental variable relationships with λs and significant transition rates were performed with the use of Pearson's correlation and linear regression using R 2.1.1.

Results

Density Dependence

A positive relationship was found between tansy ragwort density and λ for all of the environments combined ($P < 0.001$), and individually for the burned and salvage-logged environment ($P = 0.025$) (Figure 4.1). This was contrary to the expected density-dependence that would show decline in λ with increased intra-specific density. However, densities were never high enough (< 200 plants m^2) to get the negative effect on population growth.

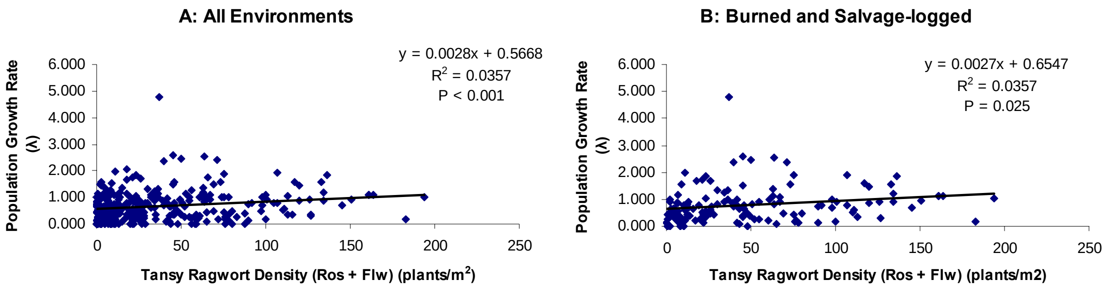


Figure 4.1. Density of tansy ragwort (t_{n-1}) versus λ (t_n) of all populations sampled in each environment ($n = 327$) (A), and the burned and salvage-logged environment ($n = 140$) (B).

Inter-specific density was investigated with percent cover of species other than tansy ragwort from 2001, 2002, and 2004 and the percent sky measurements from 2004 were used to assess total vegetation (intra- + inter-specific) influences on population growth (Table 4.1).

Table 4.1. Mean (± standard deviation) of the 2004 ocular estimates of percent cover of other plant species and the mean (± standard deviation) of the measured percent sky.

Environment	Cover of Other Plant Species (%)	Percent Sky (%)[a]
Burned and Salvage-logged	24.3 (23.18)	48.07 (19.81)
Burned and Salvage-logged	42.8 (24.32)	53.33 (21.83)
Burned and Salvage-logged	59.4 (30.72)	32.94 (5.63)
Burned and Salvage-logged	43.5 (21.24)	70.04 (16.76)
Burned	56.8 (24.39)	48.99 (12.45)
Burned	61.6 (29.28)	53.60 (14.67)
Burned	55.9 (29.56)	47.92 (15.12)
Burned	24.2 (22.13)	47.80 (21.36)
Burned	60.9 (32.45)	66.11 (21.52)
Meadow	80.0 (14.27)	47.08 (12.56)

[a] Percent Sky from LAI – 2000 Plant Canopy Analyzer, LI – COR = fraction of sky that is not blocked by foliage.

Linear regression identified a significant relationship between the percent cover of species other than tansy ragwort and λ. The over summer survival of tansy ragwort rosettes for all of the environments combined was also shown to decline with increasing cover of species other than tansy ragwort (P = 0.004, and P = 0.003, respectively) (Figure 4.2 and 4.3, respectively).

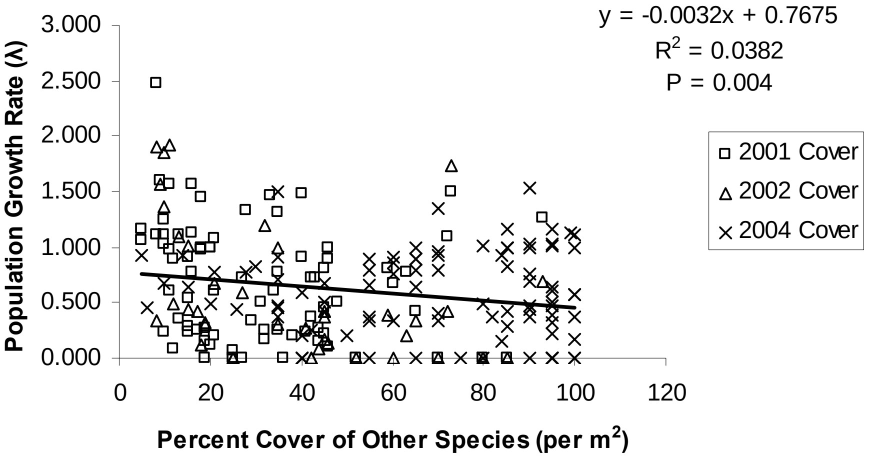


Figure 4.2. Percent cover of species other than tansy ragwort (t_{n-1}) versus projected tansy ragwort λ (t_n) for all populations sampled in each environment (n = 212).

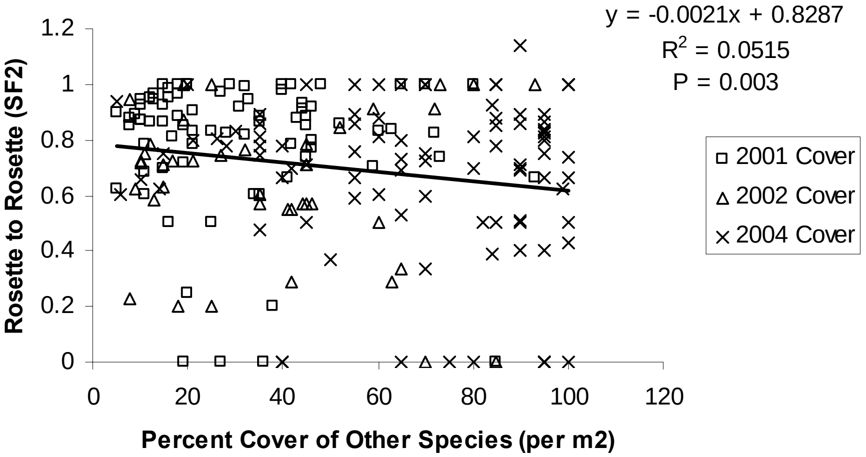


Figure 4.3. Percent cover of species other than tansy ragwort (t_{n-1}) versus the over summer tansy ragwort rosette survival (t_n) for all populations sampled in each environment (n = 212).

No significant relationships were found between the 2004 measurements of percent sky and the tansy ragwort λ_{2005}.

Environmental Variables

The relationship between soil characteristics and tansy ragwort population important transition rates was investigated first by using Pearson's correlation followed by linear regression (Table 4.2). Each of the soil samples from the plots in different environments had similar amounts of percent sand, silt, and clay and similar amounts of CEC (Appendix F.1).

Pearson's correlation (Appendix F) indicated no significant relationships between soil P, and K and 2002 over winter and over summer survival of rosette (FS2 and SF2) when data from all environments were combined. Additionally, no significant relationships were found with the Pearson correlations for the 2001 through 2005 over winter and over summer survival of rosette (FS2 and SF2) with total N, OM, pH, or CEC.

Table 4.2. Mean (± standard deviation) of selected 2002 soil properties of burned and salvage-logged (n = 40), burned (n = 40), and non-burned meadow environment plots (n = 5).

Environment	N (ppm)	P (ppm)	K (ppm)	OM (%)	PH	CEC (meq/100g)
Burned and Salvage-logged	2.7 (0.82)	43.6 (22.61)	224.0 (97.76)	5.2 (3.56)	6.5 (0.63)	12.3 (5.33)
Burned and Salvage-logged	2.2 (0.42)	73.6 (35.89)	155.2 (50.62)	2.5 (1.74)	6.3 (0.40)	7.4 (2.50)
Burned and Salvage-logged	2.7 (0.95)	45.3 (23.72)	143.8 (28.54)	6.8 (4.69)	6.2 (0.49)	12.1 (2.40)
Burned and Salvage-logged	2.7 (0.48)	97.5 (31.88)	219.7 (56.34)	3.6 (0.88)	6.1 (0.58)	10.8 (1.26)
Burned	1.9 (0.32)	45.0 (31.25)	159.3 (45.62)	3.1 (3.13)	6.4 (0.63)	8.1 (2.07)
Burned	2.0 (0.47)	30.0 (21.73)	138.1 (29.79)	9.9 (11.11)	5.8 (0.65)	14.0 (5.76)
Burned	2.5 (0.97)	47.7 (20.20)	162.2 (68.16)	3.2 (1.80)	6.4 (0.65)	9.9 (3.59)
Burned	1.1 (0.32)	40.6 (24.37)	151.6 (61.18)	2.8 (1.64)	6.0 (0.32)	7.7 (1.92)
Meadow	1.0 (0.00)	45.6 (14.29)	162.2 (16.22)	7.9 (5.09)	5.6 (0.18)	11.7 (4.31)

Pearson correlation of -0.619 (Appendix F) suggested a significant negative relationship between previous year mean precipitation and rosette over winter survival (FS2) in the meadow environment. This relationship was quantified with a significant regression analysis (P = 0.001) (Figure 4.4).

A significant decline was detected in the over winter survival (SF2) of tansy ragwort rosettes over the time period of the study in the meadow environment (P = 0.003) (Figure 4.5), and in the burned and salvage-logged environment (P = 0.002) (Figure 4.6).

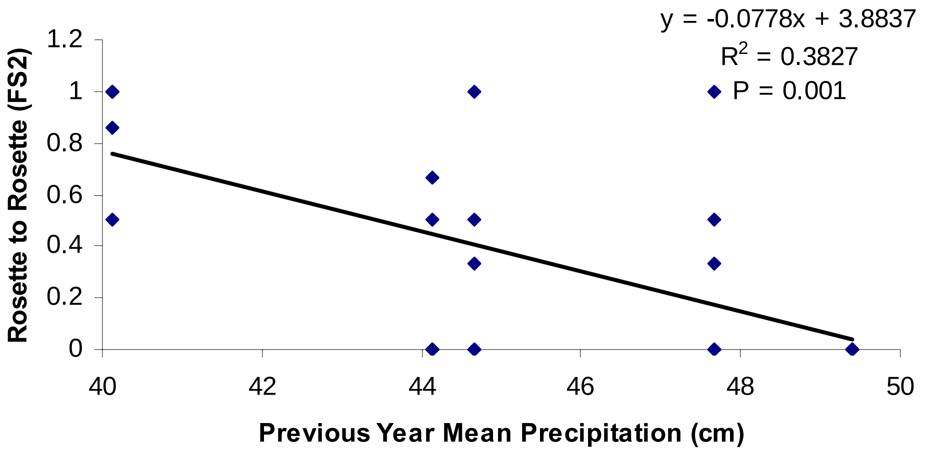


Figure 4.4. Relationship of rosette-to-rosette over winter survival transition rate (FS2) and previous year precipitation for the meadow environment (n = 25).

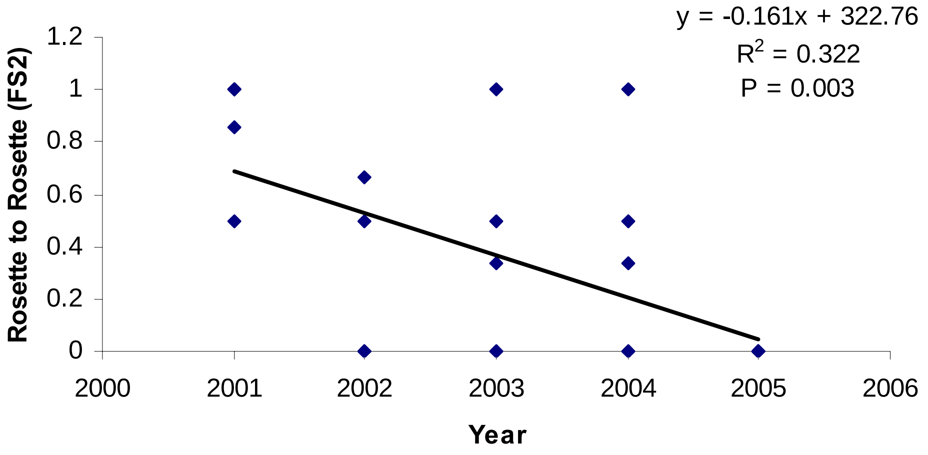


Figure 4.5. Relationship between rosette-to-rosette over winter survival transition rate (FS2) and time for the meadow environment (n = 25).

Several other relationships ($\alpha = 0.05$) were suggested using the Pearson correlation matrix for transitions rates other than rosette survival. With all three environments combined the rosette to flowering plant transitions (SF3) were negatively related to the previous and current year precipitation, and the year (r = -0.270, r = -0.196, and r = -0.252, respectively). Pearson correlation suggested that seedling-to-rosette (SF1) and spring seedling emergence

(FS5) were negatively related to previous year precipitation and to year (r =-0.236, r = -0.216, and r = -0.252, respectively). Additionally, fall seedling emergence (SF4) and seed production (SF6) may be positively related to current year precipitation (r = 0.230, and r = 0.242, respectively).

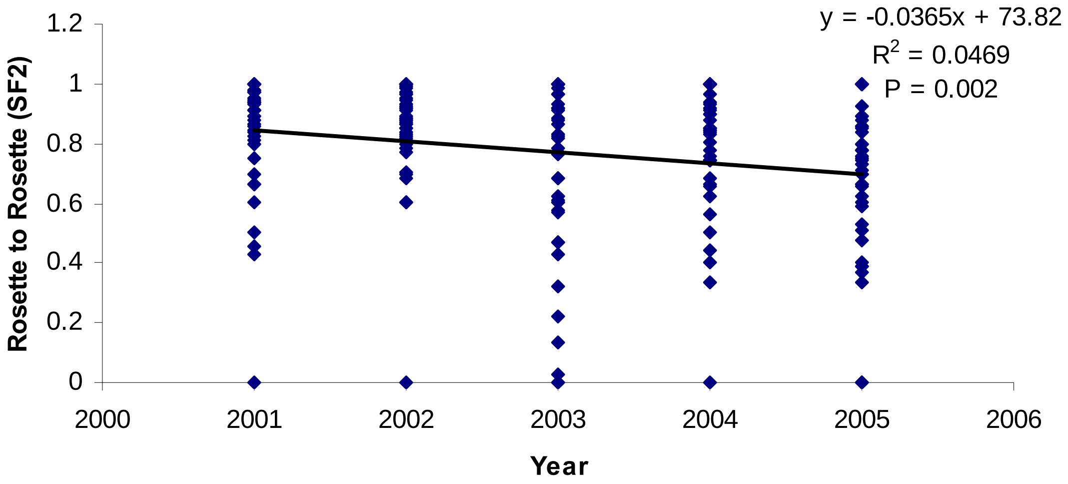


Figure 4.6. Relationship between rosette-to-rosette over summer survival transition rate (SF2) and time for the burned and salvage-logged environment (n = 200).

Discussion

The positive relationship between tansy ragwort population growth and mature plant density indicated that tansy ragwort densities were not high enough to be decreasing population growth in any of the environments where it was found. Population densities would have to increase before intra-specific density dependence would significantly reduce the λ. In results that were consistent with Trainor (2003), inter-specific abundance showed a significant negative relationship between the projected λ of tansy ragwort and the cover of species other than tansy ragwort when all environments were combined. Additionally, inter-specific density dependence reduced the rosette survival with increased cover of species other than tansy ragwort. However, no relationships were found for the percent sky measurement from 2004 and the λ in 2005 indicating that populations are not responding with an expected increase in λ to increasing amounts of open canopy.

Trainor (2003) found a significant negative relationship between rosette winter survival (FS2) for 2002 and the soil CEC, and percent organic matter. However, when this same relationship was reinvestigated with more FS2 transition rates from more years (2001 through 2005); the relationship was no longer significant. Thus, it was concluded that the soil characteristics measured were not related to the important demographic processes for tansy ragwort populations. Yearly precipitation was significantly related to the rosette survival of tansy ragwort in the meadow environment indicating that in dry years rosettes survival increased, counter to what was expected given tansy ragwort's historically maritime distribution. Additionally, the year that transitions were recorded was shown to be negatively related to rosette survival in both the burned and salvage-logged and the meadow environment.

In Britain and Western Europe tansy ragwort is a late successional species (van der Meijden 1974) but it can also be abundant in pioneer to mid seral communities at newly disturbed sites (Harper and Wood 1957). At our study site, tansy ragwort population densities were below that which intra-specific density dependence would lower the λ or rosette survival, indicating that something other than intra-specific density dependence was keeping tansy ragwort population densities low. The λ and rosette survival of tansy ragwort was negatively related to increased percent cover of other species, and increased time since the wildfire. Therefore, tansy ragwort populations may respond with an increase in the λs and density following wildfire disturbance, but as time from the wildfire disturbance increased in our study and native vegetation recovered following the wildfire of 1994 and subsequent salvage logging, tansy ragwort λs and rosette survival decreased. Thus, the tansy ragwort population dynamics in northwestern Montana is indicative of a classic ruderal species responding to disturbance rather than a late successional species that will be maintained as native vegetation recovers following disturbance.

Management Implications

Our results and those from Trainor (2003) identify tansy ragwort as a ruderal species. Therefore, disturbance in the form of wildfire exacerbated by salvage logging are an invitation for tansy ragwort colonization and population growth if within range of source populations. However, as the area recovers with increased time from a disturbance event, minimizing any management that causes disturbance will be a good preventative strategy. Tansy ragwort management should shift from concentrating on control to increased population monitoring to more specifically identify the environmental conditions where populations can become most invasive and act as sources for new colonization. Management that might cause disturbances should be used only for populations that have been increasing in density. Instead of managing for the reduction of tansy ragwort with direct methods such as the application of herbicide or release of biological control agents, managers could reduce the λ and the rosette survival by increasing native cover. Harper and Wood (1957) found that competition from surrounding plants may increase seedling mortality. Efforts to improve the other species' cover in areas with tansy ragwort could include revegetating tree species at a higher density and thinning trees only after the local extinction of tansy ragwort.

CHAPTER 5

THE ROLE OF SLASHPILE BURNS IN THE ESTABLISHMENT OF TANSY RAGWORT POPULATIONS

Introduction

The harvest of timber results in woody debris (slash) that is unsuitable for use as lumber. Similarly, thinning of small diameter trees creates large quantities of slash. Frequently the slash produced in either situation is gathered into large piles near roads and removed through chipping or burning (Smith et al. 1997). Burning is the favored method of slash removal, because it enables land managers to safely burn under a broad range of weather conditions (Hardy 1996).

Large amounts of anecdotal evidence reports that the burning of slash can assist the spread and establishment of non-indigenous species (NIS) and ruderal plant species (Dickinson and Kirkpatrick 1987). However, very few studies have quantified the effects of burning slashpiles on NIS establishment. Additionally, the conflicting results from the few existing field studies of slashpile burns and controlled laboratory studies, limits the usefulness of the information for land managers.

In a review of the effects of fire on belowground systems, Neary et al. (1999) reported that heating soil for a long duration, similar to what would occur when a slashpile was burned, cause severe changes to plant community successional rates, alters above- and belowground species composition, volatizes nutrients, produces rapid or decreased mineralization rates, alters C:N, and accelerates erosion, leaching, and denitrification. The soil heating is not limited only to the soil surface. The heat from burning fuel is transferred to the organic and mineral layers of underlying soils (Neary et al. 1999). The depth of penetration of heat into the underlying soil was related to the amount of accumulated fuel in a slashpile (Odion and Davis 2000). The soil temperature found at a depth of 10 cm remained at 100 ^{o}C for over 21 hours and at 40 cm below the soil surface the temperature increased nearly 20 ^{o}C from 20 ^{o}C *(*Roberts 1965). Beyond short term heating resulting from burning the slashpile, the temperature of the soil might be higher within slashpile burned areas than surrounding non-burned areas due to direct solar radiation heating on exposed soil (Neary et al. 1999).

The piling and subsequent burning of slash may cause changes in soil physical and chemical characteristics resulting in the alteration and reductions of habitat for native fauna (de Bano et al. 1998, Seymour and Tecle 2004). Soil temperatures exceeding 200 ^{o}C induces changes to the soil that are generally detrimental to the soil productivity including: volatilization, heat-induced dissolution, and mobilization of fine material (Soto et al. 1991). Even with the intense soil heating from burning slashpiles, and solar radiation heating, the damage to the soil is limited to the local area of the slashpile (de Bano et al. 1998).

Some studies have found that the soil surface heating that resulted from slash burning changed the physical structure of the soil. Neary et al. (1999) speculates that the removal of organic matter by fire at the soil surface and the top few centimeters of mineral soil decreased soil pore size, possibly resulting in increased surface water runoff and erosion, and reduced water retention within mineral soil.

Belowground ecosystems can be altered beneath a slashpile burn from direct heating and indirectly due to the changes in soil properties resulting from heating. The duration of the fire influences greatly the damage to the belowground ecosystem (Neary et al. 1999). Fires that are slow moving, or concentrated in slashpiles, impact the belowground system with more complexity and severity than fast moving fires (Neary et al. 1999).

An important component of the belowground ecosystem is the seed bank, which acts as a buffer between the seed rain and the loss of seeds due to germination, predation, or death (Harper 1977). While fire is needed for some plant species to release seeds from dormancy, Clack and Wilson (1994) found that fire decreased the soil seed bank density in old growth Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) forest communities. Fire consumed the seed bank, affecting the seed viability, and altering the germination of surviving seeds (Wang and Kemball 2005). A severe fire tends to reduce subsequent total plant coverage as a result of the reduced seed viability and altered germination (Johnston and Woodard 1985).

In general, vegetation removal and soil heating result in conditions that might enable the colonization of potentially invasive NIS (Smith et al. 1997). Korb et al. (2004) found that nearly 80 to 100 percent of the seed that remained viable within a slashpile were NIS and / or ruderal species. Additionally, the effect of slashpile burning on plant species composition might not be isolated to just the slashpile. Korb et al. (2004) found seven months after burning that 68 % of seed found three meters away from the edge of a burned slashpile were NIS.

Slashpile burning might also reduce the density and cover of native species while promoting the cover of NIS. Seymour et al. (2004) found in a study of the effects of slashpiles on a ponderosa pine (*Pinus ponderosa* Laws) plant community that native plant density decreased following the burning of large slashpiles, and NIS density and percent cover increased in areas where slashpiles were burned or manually removed. Another study found an increase in total plant cover by 68 % within the slashpile five years after burning (Haskins and Gehring 2004). The same study found that NIS were four times more abundant in burned areas than non-burned areas (Haskins and Gehring 2004).

The trend for replacement of native species by NIS following a slashpile burn does not hold for every system. Based on their study that showed very little soil chemistry change, Seymour and Tecle (2004) concluded that slashpile burning was unlikely to cause changes in floral community of a ponderosa pine dominated community.

The role of slashpiles in the occurrence of NIS introductions will likely gain attention as areas for early detection and rapid response. The disturbance created from slashpile burning might be examined as entrance points into new habitats or sources of population density expansion for NIS. Learning the effects of slashpile burning on the forest ecosystem can help assess when and where to use slashpile burning as a management tool.

Our study was designed to investigate the anecdotal based hypothesis that slashpile burns serve as an entrance point for the establishment of tansy ragwort (*Senecio jacobaea* L.) and a possible source for colonization of new environments. We tested the hypothesis by determining the relative emergence rate and survival of tansy ragwort seedlings at locations within and surrounding slashpiles. In addition, we wanted to determine if the environment immediately following fire was more conducive to population growth than we found for the populations that we studied (Chapter 3) seven years following fire.

In order to investigate these objectives the slashpiles were stratified into visibly different environmental conditions associated with the slashpile burned area. The null hypothesis was that the slashpile environmental conditions had no effect on the establishment and population dynamics of tansy ragwort. The alternative hypothesis was that the establishment and population dynamics of tansy ragwort would vary with the different conditions within the slashpile burned areas.

Material and Methods

Area Description

The field areas were located in the Little Wolf drainage on land owned by Plum Creek Timber Company within the Kootenai National Forest in northwest Montana. Within the Little Wolf drainage slashpile burning was used to remove slash from logging operations and two slashpile areas were chosen for the study. The slashpile areas included the slashpiles and surrounding non-burned vegetation. One of the slashpiles had been burned late fall to early winter of 2003 and the second slashpile had been burned late fall to early winter of 2004. Korb et al. (2004) found that the boundary of a slashpile was clearly identifiable by white ash, charred, blackened soil, and no vegetation. Following the burning of the slashpile at both the 2004 and 2005 slashpile the soil directly under the piled wood was covered with white ash, while the edges of the burn had blackened, burned duff on the soil surface. Surrounding both of the slashpiles was non-burned vegetation that was not under a forest canopy. Additionally, near the 2005 slashpile there was non-burned, undisturbed forest vegetation. There were no tansy ragwort plants visible in the slashpile areas when the experiment was established.

The slashpiles were stratified into three soil conditions, high severity burn, low severity burn, and non-burned. The stratification was achieved through visual inspection looking for a soil covered by white ash, indicating high severity burn; a soil covered with mostly lightly burned blackened duff, indicating low severity burn; or a non-burned soil cover (Parsons 2003). The non-burned area was then divided into areas that were disturbed and undisturbed. The above ground vegetation was removed with a shovel from the disturbed areas. In addition, the 2005 slashpile included an environment of non-burned undisturbed forest (under a canopy of Douglas fir). Surrounding the 2004 slashpile a fence was constructed to exclude the grazing of cattle. A cattle exclosure was not needed for the 2005 slashpile.

Seeds

Tansy ragwort seeds were obtained from plants throughout the Little Wolf drainage from previous year's seed production. Bulked seed was stored in a 4 ^{o}C refrigerator. Seeds were tested for germination prior to seeding in the field. Seeds were germinated at 19 ^{o}C for 30 days.

Seedling Environment

Tansy ragwort was seeded within each of the environments in 0.1 m^2 sample plots that were randomly placed and made permanent using stakes. Eight plots were placed in each of the four environments for the 2004 slashpile and the five environments for the 2005 slashpile (Table 5.1).

Table 5.1. Conditions and environments at each slashpile area.

Burn Environments	Number of Plots 2004 Slashpile	 2005 Slashpile
High Severity	8	8
Low Severity	8	8
Non-Burned, Disturbed	8	8
Non-Burned, Undisturbed	8	8
Non-Burned, Undisturbed Forest	-	8
Growing Season Precipitation (April - October)	32.99 cm	23.77 cm
Added Water	20.3 cm	0.0 cm
Weeded	Yes	No

Within each sample plot, 200 tansy ragwort seeds (2000 seeds / m^2) were scattered onto the soil surface in June for the 2004 slashpile and in May for the 2005 slashpile. The 2004 slashpile received 2.5 cm of water following seed dispersal. In 2004 an additional 2.5 cm of water was added twice weekly from June 19th to July 6th until new germination began to decrease, indicating that peak emergence had been reached. Plots were weeded for all seedlings other than tansy ragwort on a weekly basis through the sampling period. In contrast, the 2005 slashpile received only natural rainfall and no weeding. Total seedling emergence and mortality for each sample plot were recorded weekly for the 2004 slashpile and monthly for the 2005 slashpile until peak emergence. The 2004 slashpile was censused bi-weekly for nine weeks after peak emergence. The 2005 slashpile was censused monthly for eight weeks. To prevent the spread of tansy ragwort into the surrounding habitat from the study area, all tansy ragwort plants were removed in the fall of 2005.

Transition Rates and Seedling Survival

In the spring and fall of 2005 the location and life history stage of tansy ragwort plants in the 2004 and 2005 slashpiles were mapped onto transparency paper. The life history stage was indicated through use of symbols to represent a seedling, a rosette, or a flowering plant. The seedlings were defined as having less than five leaves, rosettes as plants with five or more leaves or a seedling present in the spring and again in the fall, and flowering plants had an inflorescence. The transparencies allowed the transition rates between life history stages of the plants to be calculated for each sample plot (Table 5.2).

Table 5.2. Explanation of the calculation of tansy ragwort life stage transition rates from the 2004 slashpile

Transition rate	Calculation	Where:
Seed bank to Seedling	sbtosdlsf = Seedlings$_{\text{fall t}}$ / 200 initial seeding rate	sbtosdlsf = number of seedlings transitioning from initial seeding rate
Seedling to Rosette	sdtorossf = Rosette$_{\text{fall t}}$ / Seedling$_{\text{spring t-1}}$	sdltorossf = number of seedlings that transitioned into rosettes from the spring census to the fall census
Rosette to Rosette	rostorossf = Rosette$_{\text{fall t}}$/ Rosette$_{\text{spring t-1}}$	rostorossf = number of rosettes that remained rosettes from the spring census to the fall census

To use the tansy ragwort difference equation model described in Chapter 3, transition rates for rosette to flowering, flowering to seed production, seed production to seed bank, seed bank to seedling, and seed bank to seed bank transitions were taken from the burned environment populations located in the near by Little Wolf fire area for the high severity burn and low severity burn and from the non-burned meadow environment for the non-burned disturbed and the non-burned undisturbed environment. With these transition rate values the difference equation model was used to estimate the population growth rate ($\lambda = N_t / N_{t-1}$) for tansy ragwort in each slashpile environment.

Climate

Climate data for the average precipitation, maximum temperature and minimum temperature for March through November for both 2004 and 2005 was collected from the Western Regional Climate Center (Figure 5.1 and 5.2).

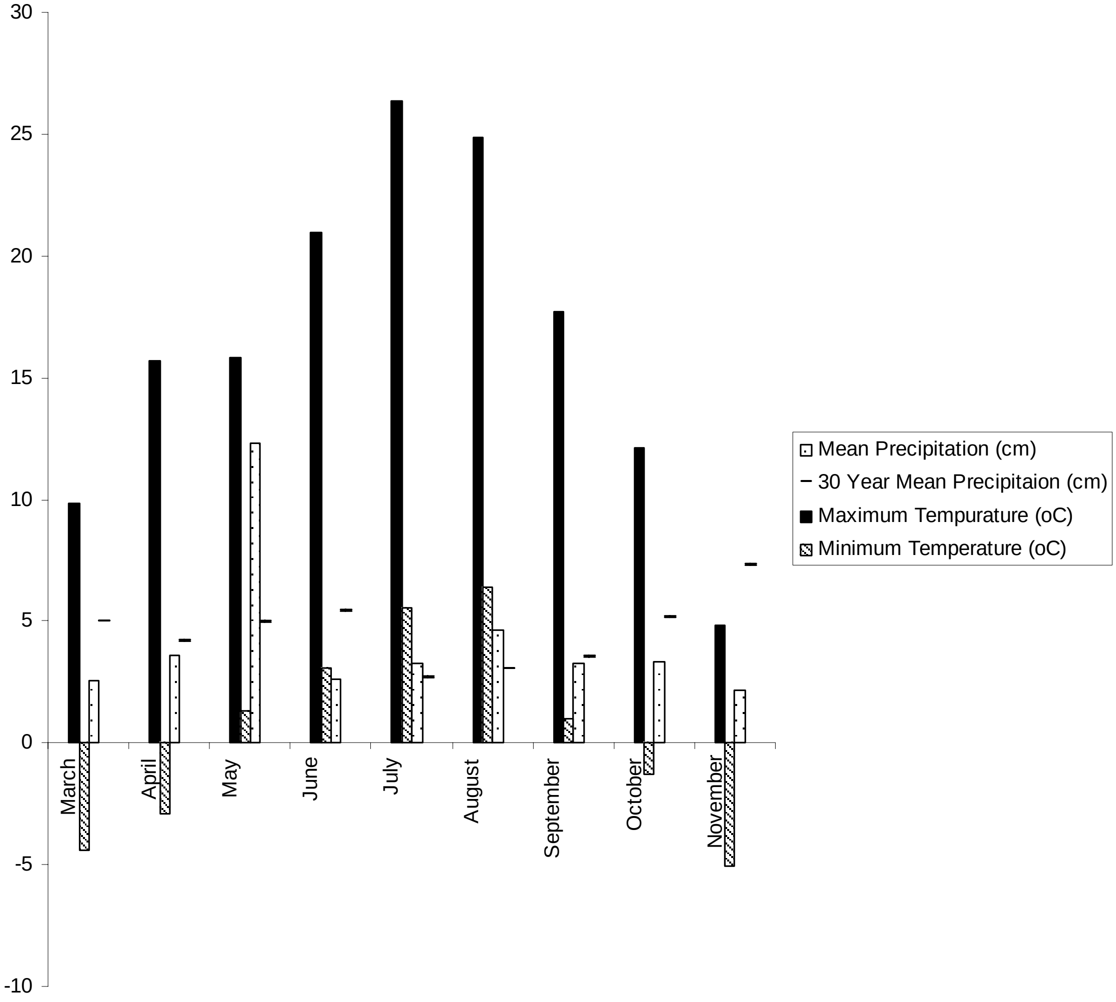


Figure 5.1. Mean monthly precipitation for 2004, 30 year mean monthly precipitation, and mean monthly maximum and minimum temperature (^{o}C) for 2004, from the Libby 32 SSE Montana weather station near the Little Wolf Creek study area.

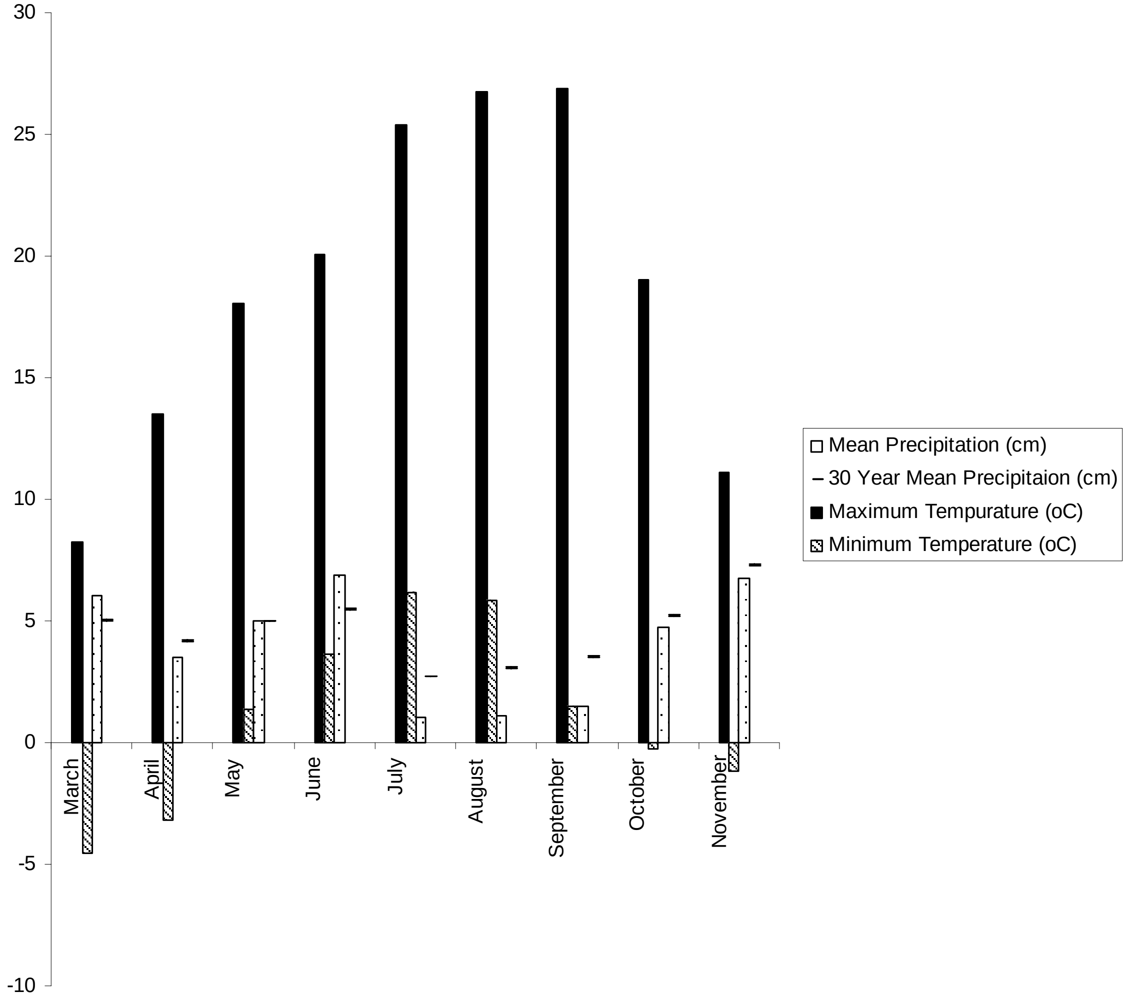


Figure 5.2. Mean monthly precipitation for 2005, 30 year mean monthly precipitation, and mean monthly maximum and minimum temperature (^{o}C) for 2005, from the Libby 32 SSE Montana weather station near the Little Wolf Creek study area.

Statistical Analysis

Multiple means comparison test in R.2.1.1 was used to test for significant differences in the emergence of seedlings (%) in each environment of the slashpiles. However, the emergence could not be investigated between slashpiles due to the differences in treatment. The Modified Levene's test was used to test for heterogeneity of variance, and the Shapiro-

Wilks test was used to test for normality of the percent emergence for each slashpile. If the data was found to have heterogeneous variance and was normal the data was tested with analysis of variance (ANOVA). The results of the ANOVA were investigated with the Tukey Honest Significance Difference with $\alpha = 0.05$ to find significant differences in percent emergence. The model calculations for the difference equation approach from chapter 3 were performed in Excel XP with programs and population analysis macros programmed by Bruce Maxwell (Appendix B).

Results and Discussion

Seed Germination Rate

Laboratory germination rates for the seeds used in the field experiments were not significantly different in 2004 and 2005 ($P = 0.080$, d.f. = 158) (Table 5.3).

Table 5.3. Mean and standard deviation of the germination rate of tansy ragwort seeds used in the slashpile experiments, but conducted in a growth chamber held at a constant 19 ^{o}C.

Year	Mean Germination (%)	Standard Deviation
2004	36.25	± 48.38
2005	50.00	± 50.32

Mean Seedling Emergence in the Field

The 2004 slashpile reached maximum seedling emergence in about 34 days after planting while the 2005 slashpile reached its maximum in about 63 days (Table 5.4). Seedlings emerged in all four of the environments planted in the 2004 slashpile, while in the 2005 slashpile no emergence was seen in the non-burned environments (Table 5.4 and Figure 5.3 and 5.4).

Table 5.4. Results of multiple means comparison of mean seedling emergence in the 2004 (d.f. = 3) and 2005 slashpile (d.f. = 4) as a function of environment (p - values).

Test	2004 Slashpile	2005 Slashpile
Modified Levene's	0.057	0.234
Shapiro-Wilks	0.243	< 0.001
ANOVA[a]	0.013	-
Environment	Mean Percent Emergence (± standard deviation)[b]	
High Severity	1.88 (2.00)^{A}	0.88 (2.09)
Low Severity	9.50 (7.42)^{B}	3.63 (7.77)
Non-burned, Soil Disturbed	4.44 (6.27)$^{A, B}$	0.00 (0.00)
Non-burned, Undisturbed	1.32 (2.47)^{A}	0.00 (0.00)
Undisturbed Forest	-	0.00 (0.00)

[a] ANOVA conducted with emergence ~ environment for untransformed data.

[b] Tukey Honest Significance Difference multiple comparison of means (α = 0.05). For mean comparison: environments with the same letter (A and B) are not significantly different with 95 % confidence.

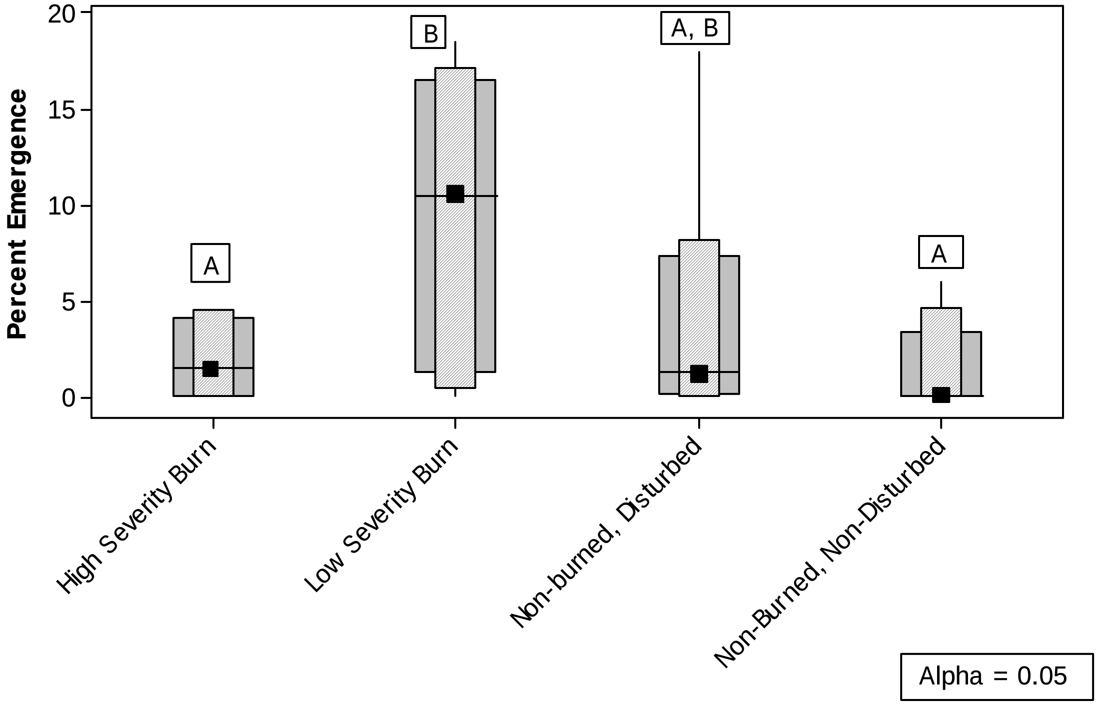


Figure 5.3. Percent emergence for the four environment types for summer of 2004 slashpile. Shown on the box and whisker plots are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. The letters represent significant difference with 95 % confidence using Tukey Honest Significance Difference.

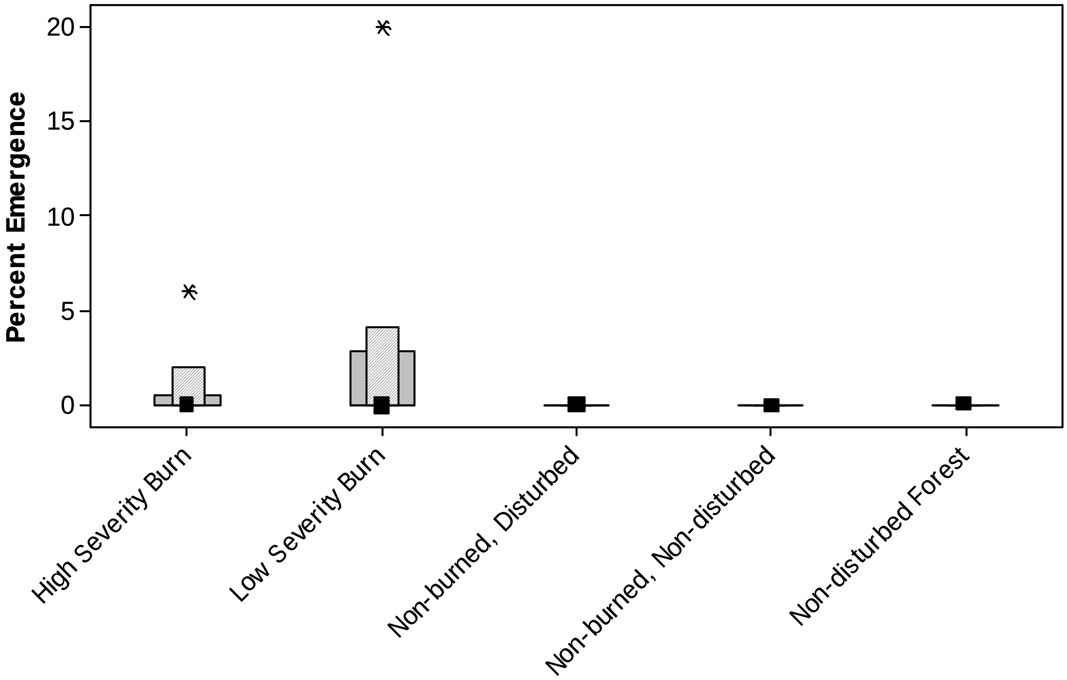


Figure 5.4. Percent emergence for the five environment types for summer of 2005 slashpile. Shown on the box and whisker plots are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments.

The results from the 2004 slashpile indicated that tansy ragwort seedling emergence rates were highly variable within environments; however a multiple means comparison indicated that emergence rates were significantly higher in the low severity burn than the high severity burn environment (Table 5.3 and Figure 5.3). In addition, the percent emergence in the low severity burned area was not significantly different than in the non-burned, disturbed. Emergence rates in the 2005 slashpile were consistently lower than the 2004 emergence rates and not normally distributed within environments and did not have homogenous variance; therefore, the multiple mean comparisons were not performed for the 2005 data. The consistent pattern in emergence rate differences between environments in the two years and slashpiles may indicate that emergence is highly limited by available water. In June and July when moisture was critical for emergence in my experiment, 2004 had above average (30 year) precipitation in June, but July was below average and there was a weekly addition of 2.5 cm of water to each plot (Figure 5.1). In 2005, June was slightly above average, but July had below average precipitation and no additional water (Figure 5.2). Given the variability in the moisture availability one can still conclude that the low severity burn environment was more conducive to tansy ragwort seedling emergence.

Plant Transition Rates

Transition rates for the population in the 2004 and 2005 slashpiles were measured from the spring of 2004 through the fall of 2005 (Table 5.5).

Table 5.5. Mean transition rate (± standard deviation) for spring 2004 to fall 2005 for plants from the 2004 and 2005 slashpile.

	2004 Slashpile			2005 Slashpile	
Environment	Seed bank to Seedling	Seedling to Rosette	Rosette to Rosette	Seed bank to Seedling	Seedling to Rosette
High Severity	0.02 (0.002)	0.13 (0.354)	0.25 (0.463)	0.01 (0.021)	0.38 (0.518)
Low Severity	0.10 (0.007)	0.25 (0.463)	0.21 (0.396)	0.04(0.078)	0.31 (0.441)
Non-burned, Soil Disturbed	0.04 (0.006)	0.09 (0.265)	0.13 (0.396)	0.00 (0.000)	0.00 (0.000)
Non-burned, Undisturbed	0.01 (0.002)	0.00 (0.000)	0.00 (0.000)	0.00 (0.000)	0.00 (0.000)
Undisturbed Forest	-	-	-	0.00 (0.000)	0.00 (0.000)

The non-burned environments in the 2005 slashpiles had transitions rates for the seed bank to seedling of zero (no emergence). This indicates seedling emergence was not recorded for the seeding density of 200 seeds / 0.1 m^2. However, had the seed density been higher or had the sample area been greater transitions rates might have been detected. For example, a transition rate of less than one plant emerging out of the 200 seeds placed in the soil (emergence rate $< 0.05 / m^2$) would have been missed.

Not all seedlings that emerged survived until the last survey of the fall in 2005 (Table 5.6).

Table 5.6. The mean and standard deviation of percent survival of tansy ragwort plants for the 2004 and 2005 slashpile.

	2004 Slashpile						2005 Slashpile	
	Spring 04 to Fall 04		Spring 04 to Spring 05		Spring 04 to Fall 05		Spring 05 to Fall 05	
Environment	Mean Survival (%)	Standard Deviation	Mean Survival (%)	Standard Deviation	Mean Survival (%)	Standard Deviation	Mean Survival (%)	Standard Deviation
High Severity	5.6	± 15.74	5.6	± 15.74	6.9	± 19.64	35.4	± 49.15
Low Severity	5.9	± 13.10	8.3	± 18.20	8.8	± 16.42	31.4	± 44.08
Non-burned, Soil Disturbed	39.2	± 70.05	2.5	± 7.07	6.7	± 12.85	0.0	± 0.00
Non-burned, Undisturbed	2.1	± 5.89	0.0	± 0.00	0.0	± 0.00	0.0	± 0.00
Undisturbed Forest	-	-	-	-	-	-	0.0	± 0.00

None of the seedlings in the non-burned undisturbed populations in the 2004 slashpile survived until the last survey in 2005. Clearly, disturbance is required for tansy ragwort to become established. However, the plants survived in the high severity burned, the low severity, and the non-burned disturbed soil environment until fall of 2005. Additionally, the high severity and low severity burned environments in the 2004 slashpile had higher survival rates at the end of 2005 than were recorded in 2004. These results suggest that the burning of slashpiles creates fringe environments immediately following burning that allow establishment of a few tansy ragwort plants from an initial population of 200 seed placed in the seed bank.

Though not statistically significant, the low severity burn environment appeared to be the best condition for seedling emergence and survival. Low severity burn is often the most prevalent environment following wildfire. Thus, the years immediately following forest wildfires are the most likely areas for tansy ragwort establishment, but at low rates.

Simulated Population Growth Rate

The transition rates were used to calculate the λ in each of the slashpile environments in 2004 and 2005 (Table 5.7).

Table 5.7. Median λ for each environment in the 2004 and 2005 slashpiles using environment specific parameter values in the difference equation model and running a Monte Carlo simulation of population growth.

Environment	2004 Slashpile		2005 Slashpile	
	Median λ	Prob. (λ_{env}) > 1.0	Median λ	Prob. (λ_{env}) > 1.0
High Severity Burn	0.00	0.000	0.46	0.000
Low Severity Burn	0.00	0.000	0.67	0.000
Non-Burned, Disturbed	0.00	0.000	0.00	0.000
Non-Burned, Undisturbed	0.00	0.000	0.00	0.000
Undisturbed Forest	-	-	0.00	0.000

The simulation of the population dynamics of tansy ragwort in the 2005 slashpile showed that the low severity burn had the highest estimated median λ. However, all λs indicated that the populations would not become locally naturalized in any of the environments. The two non-burned environments in the 2004 slashpile with very low emergence rates had estimated λs of 0. However, the non-burned slashpile populations used transition rates from the meadow environment (Chapter 3) for the transition rates not associated with seedling emergence and survival. These transition rates might have under-estimated the potential growth for the non-burned environments associated with the slashpiles. Additionally, greater differences in the growth rate might have become apparent had the study been lengthened or had the transition rates come from populations in more disturbed environments like those adjacent to the slashpiles rather than the undisturbed meadows (described in Chapter 3).

The simulation of the population dynamics of tansy ragwort in the two slashpiles was repeated with increased level of seed input and increasing the emergence rates for all environments above 0 to values that might have been detected if we had used more seeds in our experiment (i.e. emergence rate < 0.005 seedlings / m^2) (Table 5.8).

Even when the simulation increased initial seed input and seedling emergence, no populations had a projected growth rate indicating the populations would locally naturalize. These finding are consistent with our elasticity analysis indicating that seed input and seedling emergence were not important to the λ of tansy ragwort (Chapter 3). The results of the simulated λs suggest that the burning of slashpiles does not immediately (first 1 year following burn) represent conditions for tansy ragwort populations to become established and invasive or, become a source of new populations.

Table 5.8. Mean and standard deviation for λ with increased seed input (200,000 / m^2) for each environment and emergence rates for non-burned environments in the 2004 and 2005 slashpiles using environment specific parameter values in the difference equation model and running a Monte Carlo simulation of population growth.

		Emergence Rates / m^2					
		0.011			0.049		
Year	Environment	Mean	Standard Deviation	Prob. (λ_{env}) > 1.0	Mean	Standard Deviation	Prob. (λ_{env}) > 1.0
2004	High Severity	0.08	± 0.196	0.000	0.09	± 0.204	0.000
	Low Severity	0.16	± 0.264	0.000	0.18	± 0.276	0.000
	Non-burned, Soil Disturbed	0.00	± 0.000	0.000	0.00	± 0.000	0.000
	Non-burned, Undisturbed	0.00	± 0.000	0.000	0.00	± 0.000	0.000
2005	High Severity	0.41	± 0.320	0.000	0.42	± 0.322	0.000
	Low Severity	0.59	± 0.309	0.000	0.59	± 0.303	0.000
	Non-burned, Soil Disturbed	0.00	± 0.000	0.000	0.00	± 0.000	0.000
	Non-burned, Undisturbed	0.00	± 0.000	0.000	0.00	± 0.000	0.000
	Undisturbed Forest	0.00	± 0.000	0.000	0.00	± 0.000	0.000

Management Implications

The results from the two years of slashpile seeding showed that tansy ragwort populations are not invasive ($\lambda > 1.0$) in the slashpile areas after one or two years when populations are started from 200 seeds / 0.1 m^2. Additionally, even with higher levels of initial seed input the simulated λs indicated that the populations would not become naturalized. These results are not consistent with the observations of managers. Possible explanations for this apparent difference include that the seed dispersal time in this experiment (spring) differs from the natural seed dispersal (fall) and emergence period. In addition, only fresh slashpiles were tested where ash was still not settled. We tried to account for seeding in June for the 2004 slashpile by adding additional water on a twice weekly basis but even with the additional 20 cm of water the populations were still not invasive.

The results from this study, though not in total agreement with the observations of managers, suggest that the population explosion that created new populations in the study area following the 1994 Little Wolf wildfire occurred after the first couple of years of establishment, but before populations were measured in 2000 (Chapter 3). In fact, the prevailing evidence from our studies showed that tansy ragwort populations were in decline in the period 7 to 11 years following the wildfire. The expansion of the tansy ragwort populations in the Little Wolf drainage that must have occurred for the populations to be found throughout the drainage might have occurred infrequently and during years with above average precipitation. Therefore, managers should monitor slashpile locations for establishment of tansy ragwort populations for the first couple of years following burning without applying management before deciding whether the populations will increase in density and thus require management.

CHAPTER 6

THE IMPACT OF AN INTRODUCTED SEED PREDATOR FLY AND FOLIAGE HERBIVORE ON POPULATION GROWTH RATES OF TANSY RAGWORT IN DIFFERENT ENVIRONMENTS

Introduction

The aim of biological control is reducing and maintaining populations of non-indigenous species (NIS) below an economic threshold (McEvoy et al. 1993). Biological control of NIS should be improved with developments in the ability to predict the population dynamics of plant populations under herbivory, granivory, and predation as well as plant compensation capacity (Cox and McEvoy 1983). Knowing the dynamics of the target plant population should help select biological control agents that target weakness in the life history of the plant populations and help determine which biological control agents to focus on for redistribution (McEvoy and Coombs 2000).

A matrix model constructed by Shea and Kelly (1998) tested the impact of biological control and other management strategies on nodding thistle (*Carduus nutans* L.) in New Zealand. With their single species, stage-structured matrix model, Shea and Kelly (1998) were able to confirm that the nodding thistle populations were increasing at two sites and with elasticity analysis show that the seed to seedling and small plant to seed transition rate were most important to the population growth. Additionally, they showed with a matrix model simulation of attack by the nodding thistle receptacle weevil (*Rhinocyllus conicus)* biological control agent that a seed loss of about 69 % would be required to decrease the nodding thistle population size in New Zealand (Shea and Kelly 1998).

Once a control organism has been released, introduction is generally irreversible (McEvoy and Coombs 2000). Before introduction it is important to know if the biological control agents are both effective and ecologically safe (Louda and Stiling 2004). Because, predicting indirect interactions of the biological control agents and the effect on non-target species is not easily obtained (Strauss 1991), models could play a crucial role in the pre-release assessments of biological control agents.

Three insects have been studied as biological control agents for tansy ragwort (*Senecio jacobaea* L.) populations in the United States; including the ragwort seed head fly (*Pegohylemia seneciaell* Meade), the flea beetle (*Longitarsus jacobaeae* Waterhouse) and the cinnabar moth (*Tyria jacobaeae* L.) (Watt 1987b). The combined attack of the cinnabar moth and the flea beetle have been cited as controlling tansy ragwort populations in California (Mastrogiuseppe et al. 1983, Pemberton and Turner 1990), Oregon (Hawkes 1981, McEvoy 1985), Washington (Piper 1985) and partial control in Canada (Julien 1987).

The primary goal of this study was to determine the impact of an introduced seed predator and foliage herbivore on the population growth rates (λ_{env}) of tansy ragwort in different environments of the study area in northwest Montana. This study is somewhat unique because the plant population demographics were assessed for 3 years prior to arrival of the biological control agents and for 2 years after their arrival on some populations. The monitored biological control agents were the cinnabar moth, and the ragwort seed head fly. We wanted to know how the biological control agents affect the demographics (transition between life history states, seed production and vegetative reproduction) and the λ of tansy ragwort populations. Starting in 2004 this objective was addressed with the incorporation of data from the biological control agents into an ongoing population invasibility analysis (PIA) (Chapter 3). The PIA including a life history model for tansy ragwort populations that was initially parameterized beginning in 2001 in three broad environmental conditions: 1) areas burned by the Little Wolf wildfire of 1994, 2) areas burned by the same wildfire and then salvage-logged, and 3) non-burned meadow. The PIA was based on a series of difference equations (Chapter 3) parameterized with field data collected from the spring of 2001 until the fall of 2005. The null hypothesis was that tansy ragwort λ would not differ with the addition of the biological control agents. The alternative hypothesis was that the λ would be different with the addition of the biological control agents and the degree of influence on the target populations could be quantified.

Materials and Methods

The field areas where populations were observed were described in chapter 3. The field sites were located 120 km southeast of Libby, Montana. All of the areas were within the area burned by the Little Wolf wildfire of 1994. Following the 1994 wildfire some burned areas were salvage-logged with 90 to 95 % of the logging completed within two years following the wildfire (Friedman, Plum Creek Lumber Co. land manager, personal communication, December 5, 2005).

The impact of the introduced biological control agents on the λs of the tansy ragwort in different environments was assessed beginning in 2004. Several biological control agents were released in the study area prior to 2004 and continuing through the remainder of the study. Assessment of the impact of the introduced predators on tansy ragwort began in 2004 once populations of the agents appeared in the established plots used to monitor the population dynamics of tansy ragwort (Chapter 3).

The ragwort seed head fly has established in the study area in all three of the environments. Starting in 2004 the same random samples of ten inflorescence per transect that were used to estimate seed productions (Chapter 3) were also used to assess the amount of tansy ragwort seed consumed by the ragwort seed head fly.

The cinnabar moth began to appear in three transects in two environments starting in 2004. The cinnabar moth appeared along two transects in the burned and one transect in the burned and salvage-logged environment. Five plots were randomly selected at the two transects where the moth was anticipated to be present at densities that might influence tansy ragwort population demographics. These plots were sprayed with *Bacillus thuringiensis* (BT) insecticide to exclude or reduce the herbivory of tansy ragwort by cinnabar moths. One of these transects was located in a burned and the other in a burn and salvage-logged environment. BT affects cinnabar moths at the caterpillar stage and causes moth mortality (Swadener 1994). Results from Rosalind et al. (1993) indicated that feeding by cinnabar moth was adversely affected by a low concentration of BT, but mortality resulted only with a high concentration of BT. Therefore, BT was sprayed at a high concentration of 24 ml of BT to 1.0 L of H_20 until the plants were saturated. The plots were sprayed weekly and in some cases bi-weekly from before the time when cinnabar moth caterpillars were observed on untreated plants, to after the caterpillars were observed to pupate on untreated plants. We assumed that the cinnabar moth would attack the non-sprayed plots while the sprayed plots would be protected from attack. However, the cinnabar moth was observed on both BT sprayed and non-sprayed plots drawing into question the effectiveness of the treatment. The cinnabar moth was also found along a third transect in 2005. None of the tansy ragwort populations on this transect, located in the burned environment, were sprayed with BT because the presence of the cinnabar moth was not anticipated. For this transect herbivory by the cinnabar moth was noted during the fall 2005 census. The population dynamics of tansy ragwort was compared within a population before attack and after attack by cinnabar moth.

Transition Rates

In 2004 and 2005 the presence of herbivory by the ragwort seed head fly and the amount of non-attacked, remaining seed were recorded per capitulum for the three environments. The number of seed produced in an attacked inflorescence was compared with the seed production by capitula on the same plants that were not attacked. These samples were used to estimated the mean tansy ragwort seed production for non-ragwort seed head fly attacked capitula, for ragwort seed head fly attacked capitula seed production, and rate of capitula attack. The meadow environment had no seed production for either 2004 or 2005. The effect of the ragwort seed head fly on the tansy ragwort λ was estimated with the model of population dynamics by reducing the seed production rate by the maximum observed seed herbivory rate.

The λ of tansy ragwort populations with cinnabar moth herbivory were obtained using transition rates values for each population before attack and after attack for the same population. Transition rate values were from 2001 through 2005.

Population Growth Rate

The λ for tansy ragwort with the addition of biological control agents was estimated using the difference equation approach outlined in Chapter 3. To test the effect of reducing the seed production on the λ, the λs were calculated using the total seed production on non-attacked plants for 2004 and 2005 and with seed production values reduced by the maximum recorded attack rate in the study area.

The effect of the cinnabar moth on the λ of tansy ragwort was estimated for the same population before and after cinnabar moth herbivory using transition rates from Chapter 3. The plots that were attacked within the transects were noted and the impact of the cinnabar moth on the λ of tansy ragwort in each environment was estimated through an additional simulation for the λ of attacked populations based on transition rates calculated before attack and transition rates calculated during and after attack. Since cinnabar moth consumes the leaves and the floral parts of tansy ragwort (Cox and McEvoy 1983), a maximum effect of the biological control on the λ was estimated by not including compensatory regrowth of floral parts. Therefore the plant seed production for attached plants was set to zero, eliminating any combined attack effect of both the cinnabar moth and the ragwort seed head fly.

Model Simulations

The transition rates for a population were randomly selected and used to simulate the population dynamics and estimate the λ of tansy ragwort. Because the variability of the λs for each environment being high and non-normally distributed, we used a Monte Carlo simulation to bootstrap our estimates of the λs from before and after attack by the biological control agents. The Monte Carlo simulation created a distribution of the λs for each environment by repeating the simulation of population dynamics 1000 times per environment.

Statistical Analysis

The estimated λs were compared using box and whisker plots generated with Minitab 14.1. The box and whisker plots of the λs included 95 % confidence intervals for the median. Therefore, if the median confidence intervals for two boxes did not overlap, the λs were considered to be different with 95 % confidence. Additionally, the probability for each environment of $\lambda > 1.0$ (defined as invasive) was calculated as the proportion of the simulated iterations resulting in a λ greater than 1.0. The model calculations were performed in Excel XP with programs and population analysis macros programmed by Bruce Maxwell (Appendix B).

Results

Seed production was significantly lower for attacked capitulum than non-attacked. However, the estimated total seed attack rate for the capitulum was in all cases lower than 11 % and for most capitulum less than 5 % (Table 6.1). The simulated median estimate of the λ for the seed head fly attacked burned and salvage-logged environment populations was 0.667 and 0.500 for the burned environment if conditions that created the transition rates were to remain constant. The 95 % confidence levels for the two environments did not overlap indicating there was a significant difference in the λs for each environment ($\alpha < 0.05$) (Figure 6.1, Table 6.2).

Table 6.1. Estimated rate of ragwort seed head fly attack, mean tansy ragwort seed production per capitulum for non-attacked capitulum (± standard deviation), and mean seed production for ragwort seed head fly attacked capitulum (± standard deviation).

Year	Environment	Attack Rate (%)	Attacked Seed Production / capitulum	Non-attacked Seed Production / capitulum
2004	Burned and Salvaged-logged	2.0	43 (19.9) *	59 (9.7) *
	Burned	5.6	45 (15.5) *	59 (11.5) *
2005	Burned and Salvaged-logged	10.7	42 (15.8) *	64 (8.8) *
	Burned	2.1	40 (3.8) *	60 (7.9) *

*Comparison significant at $\alpha = 0.05$ across environments within the same year.

To provide a relevant assessment of the tansy ragwort λs with skewed distributions of λ, we calculated the probability that λ would exceed 1.0 (i.e. would show positive growth). In addition, this qualification would allow a more sensitive measure of the influence of the biological control agents. The probability that populations had λ greater than 1.0 based on the Monte Carlo simulation was 0.31 and 0.33 for non-attacked and attacked populations, respectively, in the burned and salvage logged environment. In the burned environment, the probabilities were 0.20 and 0.21, respectively (Table 6.2). In both environments, the variation was not great enough to conclude that the seed head fly had an impact on the tansy ragwort λ and that λs greater than 1.0 (invasive) are relatively rare.

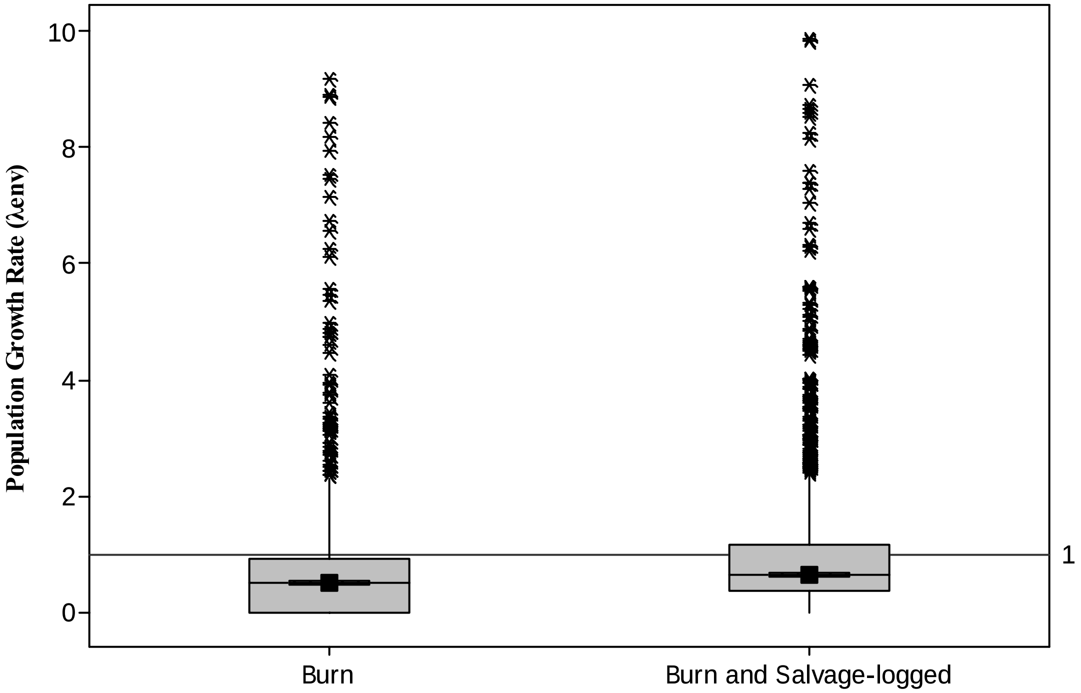


Figure 6.1. The λ of tansy ragwort when FS1 (flowering plant to seed production) had been reduced by 11 %. Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. Outliers ranging from 10 – 1627 were removed from the Burned and Salvage-logged and from 10 – 243 for the Burned environments to display the central tendency of the distribution. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

Table 6.2. Probability of λ > 1.0 and median λ based on Monte Carlo simulation by environment using the life-cycle model with reduced seed production to simulate the effect of the ragwort seed head fly.

	Without Seed head fly		With Seed head fly	
Environment	Probability λ > 1.0	Median λ	Probability λ > 1.0	Median λ
Burned and Salvage-logged (n = 40)	0.309	0.682	0.330	0.667
Burned (n = 49)	0.204	0.534	0.207	0.500

These results should not be surprising since seed production had a low elasticity value indicating low relative contribution to tansy ragwort λ (Chapter 3). However, the predation rate could increase with an increase in the population density of the seed head fly. Simulating with populations of tansy ragwort with a $\lambda > 1$, a seed predation rate of 20 percent could reverse an increasing λ.

During the course of the 2004 and 2005 field season tansy ragwort populations were attacked by the cinnabar moth in several transects (Table 6.3).

Table 6.3. Total number of populations per environment attacked by cinnabar moth during the 2004 and the 2005 field season.

Environment	2004	2005
Burn and Salvage-logged	0	1
Burn	2	4
Meadow	0	0

The simulated estimate of the tansy ragwort λ before cinnabar attack for the burned and salvage-logged environment was a median λ of 0.000, while after attack the same populations had a median λ of 0.343. The burned environment had a median λ of 1.000 before attack by the cinnabar moth, while after attack the same populations had a median λ of 0.429 (Figure 6.2, Table 6.4). Based on the median λs and the variation in the simulated data there is no reason to conclude that the populations are growing differently in the different environments. However, the effect of the cinnabar moth on the tansy ragwort λ in both environments may be significant.

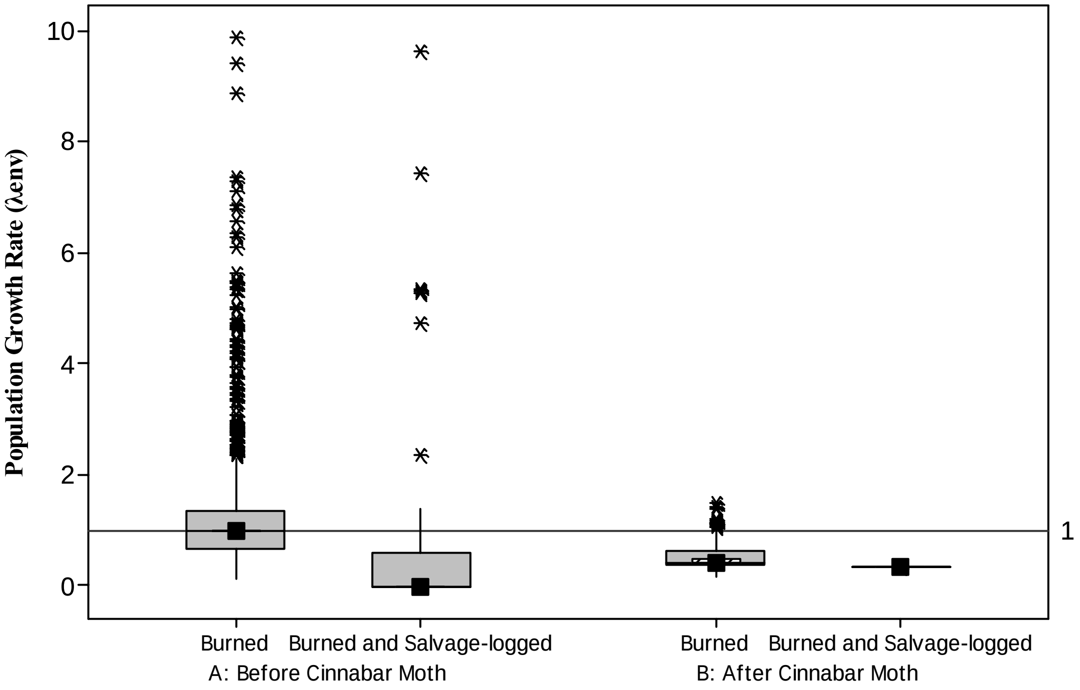


Figure 6.2. The λ of tansy ragwort for populations based on transition rates calculated for A: before plots were and attacked, and B: after plots were attacked by cinnabar moths in 2004, 2005 or both field seasons. Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. Outliers for before cinnabar moth attack ranging from 10 – 21 were removed from the Burned and Salvage-logged and the Burned environments to display the central tendency of the distribution. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

The Monte Carlo simulation results estimate the probability that populations in different environments have a λ greater than one was less for the populations after attack by the cinnabar moth (Table 6.4).

Table 6.4. Probability of $\lambda > 1.0$ and median population growth rate based on Monte Carlo simulation for the same plots before and after cinnabar moth herbivory.

	Before Cinnabar Moth		Same Plots After Cinnabar Moth	
Environment	Probability $\lambda > 1$	Median λ	Probability $\lambda > 1$	Median
Burned and Salvage-logged (n = 1)	0.019	0.000	0.000	0.343
Burned (n = 4)	0.462	1.000	0.015	0.429

However, caution needs to be used when interpreting the results due to low sample size and failure to control for environmental conditions before and after cinnabar moth attack. In addition, the affect of the cinnabar moth herbivory on the transition rates for rosette survival, rosette maturation into flowering plants, and seed production might have been affected in plots sprayed with BT insecticide that were later attacked by the cinnabar moth.

Discussion

The ragwort seed head fly significantly reduced seed production in attacked capitula of the burned and salvage-logged and the burned environments for 2004 and 2005. However, the simulated population dynamics based on the highest level ragwort seed head fly attack showed little change in the probability for each environment to have a locally increasing or invasive population ($\lambda_{env} > 1$). Yet, an increasing tansy ragwort population prior to predation could decline with increased predation rate.

The effect of the other monitored biological control agent, the cinnabar moth, indicated that a reduction in the λ of tansy ragwort might result from cinnabar moth herbivory. A significant reduction in the estimated λ was seen for populations in the burned environment. However, these result need to be viewed with caution because of the small population size of the attacked plots (n = 5), short term of attack data (1 or 2 years), uncontrolled environmental factors (e.g. amount of precipitation before and after attack), and the effect of the BT treatment (e.g. herbivory affects of the cinnabar moth on transition rates for plots sprayed with BT).

Management Implications

The value of biological control as a management tool has not fully been investigated at the study areas due to the short time frame of the observations and the small number of affected populations. However, due to the low level of importance given to seed production based on the elasticity analysis (Chapter 3), the seed head fly alone was not expected to reduce the λ significantly. These results are consistent with those reported by Burrill et al. (1994). Therefore, based on the current recorded maximum predation rates any further use and relocation of biological control agents for tansy ragwort should not include the seed head fly. However, if predation rates were to increase with increased seed head fly density, the λ tansy ragwort could be reduced.

The cinnabar moth may reduce the growth rate of tansy ragwort because of the damage to the rosette survival of the plant. However, cinnabar moth may create a risk to native *Senecio* species because it has been reported on native species including *S. triangularis* and *S. pseudaureus* (Diehl and McEvoy 1990, Fuller et al. 2001) and personally observed on *S. streptanthifolius* within the study areas (Bauer, personal observation, August, 11 2005). Therefore, given the results from Chapter 3 indicating that the populations of tansy ragwort are in general naturally in decline or not consistently increasing, the continued use of the cinnabar moth is drawn into question.

The effect of a third biological control agent, the ragwort flea beetle was not monitored within the study sites for populations had not established to a level that enabled collection on herbivory attack on the λ of tansy ragwort.

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APPENDICES

APPENDIX A

TRANSITIONS FOR VALIDATION MODEL

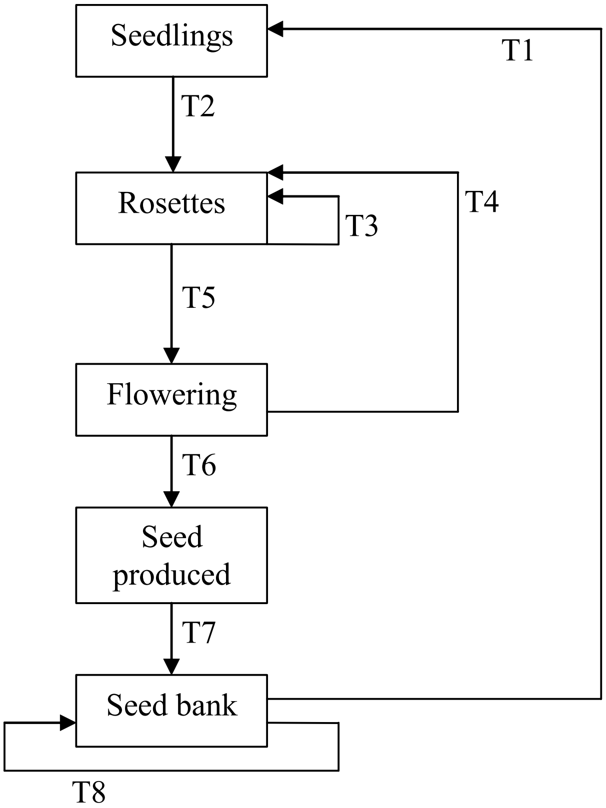


Figure A.1. Life-cycle model for tansy ragwort with one transition per year recorded used for the Lefkovitch vital rate matrix. The life history stages (states) are in squares and the arrows indicate calculated annual vital rates. Solid arrows labeled T indicate fall-to-fall vital rates.

Table A.1. Transition rate matrix of a stage-structured life-cycle model of tansy ragwort with the use of one transition per year. Matrix elements represent the probabilities that individuals in one size class year *t* –1 (columns) will enter a class year *t* (rows). Zeros indicate transition rates that do not exist or were not calculated for this study.

	Seedling	Rosette	Flowering	Seed Produced[a]	Seed Bank[b]
Seedling	0	0	0	0	T1
Rosette	T2	T3	T4	0	0
Flowering	0	T5	0	0	0
Seed Produced	0	0	T6	0	0
Seed Bank	0	0	0	T7	T8

[a] The probability for seed produced to enter the seed bank (T7) was set to 1.0 because we assumed immigration was equal to emigration.

[b] The probability for seed to remain in the seed bank was set to each area’s respective seed survival rate as found from the seed burial study explained in the text.

Table A.2. Explanation of the calculation of tansy ragwort vital rates for the life history model using one transition per year.

Vital rate	Calculation	Where:
T1	sbtosdl = Seedlings$_t$ / (seed produced$_{t-1}$ $*$ mean seed survival rate$_{\text{environmental type}}$);	sbtosdl = number of seedlings transitioning from seeds after accounting for the survival of the seed bank
T2	sdltoros = ros$_t$ / sdl$_{t-1}$	sdltoros = number of seedlings that transitioned to rosettes from the fall$_{t-1}$ census to the fall$_t$ census, sdl = number of seedlings, t = year 2001
T3	rostoros = ros$_t$ / ros$_{t-1}$	rostoros = number of rosettes that remained rosettes from the fall$_{t-1}$ census to the fall$_t$ census
T4	flwtoros = ros$_t$ / flw$_{t-1}$	flwtoros = number of flowering plants that reverted to rosettes from the fall$_{t-1}$ census to the fall$_t$ census
T5	rostoflw = flw$_t$ / ros$_{t-1}$	rostoflw = number of rosettes that transitioned to flowering shoots from the fall $_{t-1}$ census to the fall $_t$ census
T6	flwtosp = estimate of seed production	flwtosp = estimate of seed production based on the number of flowering plants/plot
T7	sptosb = 1	sptosb = number of seeds produced that reach the seed bank, estimated as 1 (migration = emigration)
T8	sbtosb = mean seed survival rate$_{\text{environmental type}}$	sbtosb = mean (standard deviation) seed bank survival rate for each environmental type

APPENDIX B

MACRO FOR TRANSITION MODEL

```
Sub transition_random_per_plot()
' transition_random_per_plot Macro
' Macro recorded 1/2/2006 by bdbauer
'
' Keyboard Shortcut: Ctrl+i
' Make sure that you change the Sheet name when you
'are doing simulations from different Sheets.
    Sheets("shf").Select
    Range("N3").Select

 Dim lam(4, 1000)

 For HabitatType = 1 To 4
   If HabitatType = 1 Then
     ht = 1
   ElseIf HabitatType = 2 Then
      ht = 2
   ElseIf HabitatType = 3 Then
      ht = 3
   ElseIf HabitatType = 4 Then
      ht = 4
 End If

   repn = Cells(4, 22)
   lamdaTot = 0
  For rep = 0 To repn
      'Select a plot within a Habitat Type at random to use its transition values
     Randomize
     plot = 0
     If ht = 1 Then
      'Get initial pop values for fall (t = 0) for habitat type 1
       SDLf = Cells(4, 15)
       ROSf = Cells(5, 15)
       FLWf = Cells(6, 15)
       SPf = Cells(7, 15)
       SBf = Cells(8, 15)
       plot = 5 + ((Int((40 - 1) * Rnd)) * 5)

     ElseIf ht = 2 Then
      'Get initial pop values for fall (t = 0)for habitat type 2
       SDLf = Cells(4, 16)
       ROSf = Cells(5, 16)
       FLWf = Cells(6, 16)
```

```
   SPf = Cells(7, 16)
   SBf = Cells(8, 16)
   plot = 205 + ((Int((50 - 1) * Rnd)) * 5)

 ElseIf ht = 3 Then
  'Get initial pop values for fall (t = 0)for habitat type 3
   SDLf = Cells(4, 17)
   ROSf = Cells(5, 17)
   FLWf = Cells(6, 17)
   SPf = Cells(7, 17)
   SBf = Cells(8, 17)
   plot = 450 + (rep * 5)

 ElseIf ht = 4 Then
  'Get initial pop values for fall (t = 0)for habitat type 4
   SDLf = Cells(4, 18)
   ROSf = Cells(5, 18)
   FLWf = Cells(6, 18)
   SPf = Cells(7, 18)
   SBf = Cells(8, 18)
   plot = 455 + ((Int((5 - 1) * Rnd)) * 5)
 End If

ngen = 20 'Cells(3, 22)
 For t = 1 To ngen
r = Int(5 * Rnd)

'Get transition values for fall to spring transitions
 sdltosdlfs = 0
 rostosdlfs = 0
 flwtosdlfs = 0
 sptosdlfs = 0
 sbtosdlfs = Cells(plot + r, 13)
 sdltorosfs = Cells(plot + r, 12)
 rostorosfs = Cells(plot + r, 10)
 flwtorosfs = Cells(plot + r, 11)
 sptorosfs = 0
 sbtorosfs = 0
 sdltoflwfs = 0
 rostoflwfs = 0
 flwtoflwfs = 0
 sptoflwfs = 0
 sbtoflwfs = 0
```

```
    sdltospfs = 0
    rostospfs = 0
    flwtospfs = Cells(plot + r, 9)
    sptospfs = 0
    sbtospfs = 0
    sdltosbfs = 0
    rostosbfs = 0
    flwtosbfs = 0
    sptosbfs = 0
    sbtosbfs = Cells(plot + r, 8)

   'Get transition values for spring to fall transitions
    sdltosdlsf = 0
    rostosdlsf = 0
    flwtosdlsf = 0
    sptosdlsf = 0
    sbtosdlsf = Cells(plot + r, 6)
    sdltorossf = Cells(plot + r, 3)
    rostorossf = Cells(plot + r, 4)
    flwtorossf = 0
    sptorossf = 0
    sbtorossf = 0
    sdltoflwsf = 0
    rostoflwsf = Cells(plot + r, 5)
    flwtoflwsf = 0
    sptoflwsf = 0
    sbtoflwsf = 0
    sdltospsf = 0
    rostospsf = 0
    flwtospsf = 0
    sptospsf = 0
    sbtospsf = 0
    sdltosbsf = 0
    rostosbsf = 0
    flwtosbsf = 0
    sptosbsf = 1#
    sbtosbsf = Cells(plot + r, 7)

  pop0 = ROSf + FLWf
     'Fall to spring transitions
      SDLs = SDLf * sdltosdlfs + ROSf * rostosdlfs + FLWf * flwtosdlfs + SPf * sptosdlfs +
SBf * sbtosdlfs
      ROSs = SDLf * sdltorosfs + ROSf * rostorosfs + FLWf * flwtorosfs + SPf * sptorosfs +
```

```
SBf * sbtorosfs
     FLWs = SDLf * sdltoflwfs + ROSf * rostoflwfs + FLWf * flwtoflwfs + SPf * sptoflwfs
+ SBf * sbtoflwfs
     SPs = SDLf * sdltospfs + ROSf * rostospfs + FLWf * flwtospfs + SPf * sptospfs + SBf *
sbtospfs
     SBs = SDLf * sdltosbfs + ROSf * rostosbfs + FLWf * flwtosbfs + SPf * sptosbfs + SBf
* sbtosbfs

    'Spring to fall transitions
     SDLf = SDLs * sdltosdlsf + ROSs * rostosdlsf + FLWs * flwtosdlsf + SPs * sptosdlsf +
SBs * sbtosdlsf
     ROSf = SDLs * sdltorossf + ROSs * rostorossf + FLWs * flwtorossf + SPs * sptorossf +
SBs * sbtorossf
     FLWf = SDLs * sdltoflwsf + ROSs * rostoflwsf + FLWs * flwtoflwsf + SPs * sptoflwsf
+ SBs * sbtoflwsf
     SPf = SDLs * sdltospsf + ROSs * rostospsf + FLWs * flwtospsf + SPs * sptospsf + SBs
* sbtospsf
     SBf = SDLs * sdltosbsf + ROSs * rostosbsf + FLWs * flwtosbsf + SPs * sptosbsf + SBs
* sbtosbsf

      'Print out first rep pop growth for each habitat type
      If rep = 1 Then
        If t = 1 Then v = 16
        v = v + 1
        Cells(v, 26) = t
        If ht = 1 Then z = 27
        If ht = 2 Then z = 28
       If ht = 3 Then z = 29
       If ht = 4 Then z = 30
        Cells(v, z) = ROSf + FLWf
      End If

      'Print out the density for each stage class in the fall at the end of selected number of
generations
      If ht = 1 And rep = 0 And t = 1 Then j = 10
      If t = ngen Then
        j = j + 1
        Cells(j, 14) = ht
        Cells(j, 15) = rep
        Cells(j, 16) = plot
        Cells(j, 17) = SDLf
        Cells(j, 18) = ROSf
        Cells(j, 19) = FLWf
```

```
          Cells(j, 20) = SPf
          Cells(j, 21) = SBf
         'Calculate population growth rate based on ROSf + FLWf
          pop = ROSf + FLWf
          If pop0 = 0 Or pop = 0 Then
            lamda = 0
          Else
            lamda = pop / pop0
          End If
          Cells(j, 22) = lamda
        End If
      Next t
      lamdaTot = lamdaTot + lamda
      lam(ht, rep) = lamda
    Next rep
    lamdaMean = lamdaTot / repn

   If ht = 1 Then
     Cells(10, 24) = lamdaMean
    ElseIf ht = 2 Then
      Cells(11, 24) = lamdaMean
    ElseIf ht = 3 Then
      Cells(12, 24) = lamdaMean
    ElseIf ht = 4 Then
      Cells(13, 24) = lamdaMean
   End If
  Next HabitatType

'Calculate the probability that there is a difference in lamda
'between pairs of habitat types
  For ht = 1 To 4
    c12 = 0
    c13 = 0
    c14 = 0
    c23 = 0
    c24 = 0
    c34 = 0
    pgto1 = 0
    pgto2 = 0
    pgto3 = 0
    pgto4 = 0
    For rep = 1 To repn
      If lam(1, rep) > lam(2, rep) Then c12 = c12 + 1
```

```
      If lam(1, rep) > lam(3, rep) Then c13 = c13 + 1
      If lam(1, rep) > lam(4, rep) Then c14 = c14 + 1
      If lam(2, rep) > lam(3, rep) Then c23 = c23 + 1
      If lam(2, rep) > lam(4, rep) Then c24 = c24 + 1
      If lam(3, rep) > lam(4, rep) Then c34 = c34 + 1
      If lam(1, rep) > 1# Then pgto1 = pgto1 + 1
      If lam(2, rep) > 1# Then pgto2 = pgto2 + 1
      If lam(3, rep) > 1# Then pgto3 = pgto3 + 1
      If lam(4, rep) > 1# Then pgto4 = pgto4 + 1
  Next rep
 Next ht
 Cells(11, 26) = c12 / repn
 Cells(12, 26) = c13 / repn
 Cells(13, 26) = c14 / repn
 Cells(12, 27) = c23 / repn
 Cells(13, 27) = c24 / repn
 Cells(13, 28) = c34 / repn
 Cells(10, 27) = 1 - c12 / repn
 Cells(10, 28) = 1 - c13 / repn
 Cells(10, 29) = 1 - c14 / repn
 Cells(11, 28) = 1 - c23 / repn
 Cells(11, 29) = 1 - c24 / repn
 Cells(12, 29) = 1 - c34 / repn
 Cells(10, 31) = pgto1 / repn
 Cells(11, 31) = pgto2 / repn
 Cells(12, 31) = pgto3 / repn
 Cells(13, 31) = pgto4 / repn

End Sub
```

APPENDIX C

SCRIPT FOR MATRIX MODEL

```
#Rcode for Tansy Ragwort Matrix Model
##filepath <- system.file("data", "TansyRWfull.txt", package="datasets")

# project the population forward 40 time steps (generations)
endtime <- 40
repn <- 20 # number of reps
pltn <- 95 # total plots
pltna <- 40 #number of plots in environment 2 : burned and salvage-logged
pltnbb <- 50 # number of plots in environment 1 : burned
pltnb <- 90 #number of plots in environment 2+1
pltncc <- 5 # number of plots in environment 3 : meadow
pltnc <- 95 #number of plots in environment 1+2+3
envn = 3 #number of environments

#Bring in the full data file
##Q <- read.table(filepath, sep="\t", header=FALSE)
Q = read.table("TansyRWfull.txt", header=F)
#Bring in the initial (2001) population values for each plot
##filepath <- system.file("data", "popvect.txt", package="datasets")
#IP <- read.table(filepath, sep="\t", header=FALSE)
IP=read.table("popvect.txt",header=F)

#Create the transition matrix
TM <- matrix(0, nrow=5, ncol=5)
#Create a matrix to put lamda values in for each rep
lamda <- matrix(0, nrow=repn*pltn, ncol=2, dimnames = list(c(),c("Lambda",
"Environment")))#1

#Put the vector of numbers of individuals in each stage for each year in a matrix
xx <- matrix(0,nrow=5,ncol=endtime+1)

#Environment 2: Burned and Salvage-logged
for (env in 1:envn) {
if (env <= 1){

for (plt in 1:pltna) #Change Number for which rows intial pop vector comes from in data
{
 #Get the initial population vector
 xx0 <- matrix(as.numeric(IP[plt,5:9]), nrow=5, ncol=1, byrow=FALSE)

 for (j in 1:repn) {
```

```
   xx[,1] <- xx0
   for (ii in 2:endtime) {
     #Get a random uniform number between 0 and 1
     rv <- runif(1,min=0,max=1)
     #Associate the random number with one of the imported transition matrices (TM)
     # and multiply by the population vector from previous year xx[,ii-1] to create
     #a new pop. vector (xx0)
     if(rv <= .25) {
       #Get transition values from full data file and make transition matrix for yr
       yr <- 4*plt-3
       A <- Q[yr,5:29]
       TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
       xx[,ii] <- TM %*% xx[,ii-1]
       }
     else if(rv > .25)
       if(rv <= .5) {
         yr <- 4*plt-2
         A <- Q[yr,5:29]
         TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
         xx[,ii] <- TM %*% xx[,ii-1]
         }
       else if(rv > .5)
                if(rv <= .75){
           yr <- 4*plt-1
           A <- Q[yr,5:29]
           TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
           xx[,ii] <- TM %*% xx[,ii-1]
           }
       else {
        yr <- 4*plt
        A <- Q[yr,5:29]
        TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
        xx[,ii] <- TM %*% xx[,ii-1]
        }

    } #end of 40 gen. loop

    # Lambda calculated on seedbank at year 40
    lamda[repn*plt-(repn-1)+j-1,1] <- (xx[5,endtime])/(xx[5,endtime-1])
    lamda[repn*plt-(repn-1)+j-1,2] <- 2 #Label what environment

} #end of rep loop
}} #end of environment loop
```

```
#Envrioment 1: Burned
else if (env >1)
if(env <=2){
for (plt in (pltna+1):pltnb) #Change Number for which rows intial pop vector
#comes from in data
{
  #Get the initial population vector
  xx0 <- matrix(as.numeric(IP[plt,5:9]), nrow=5, ncol=1, byrow=FALSE)

  for (j in 1:repn) {
   xx[,1] <- xx0
   for (ii in 2:endtime) {
     #Get a random uniform number between 0 and 1
     rv <- runif(1,min=0,max=1)
     #Associate the random number with one of the imported transition matrices (TM)
     # and multiply by the population vector from previous year xx[,ii-1] to create
     #a new pop. vector (xx0)
     if(rv <= .25) {
       #Get transition values from full data file and make transition matrix for yr
       yr <- 4*plt-3
       A <- Q[yr,5:29]
       TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
       xx[,ii] <- TM %*% xx[,ii-1]
       }
     else if(rv > .25)
       if(rv <= .5) {
         yr <- 4*plt-2
         A <- Q[yr,5:29]
         TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
         xx[,ii] <- TM %*% xx[,ii-1]
         }
       else if(rv > .5)
                   if(rv <= .75){
           yr <- 4*plt-1
           A <- Q[yr,5:29]
           TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
           xx[,ii] <- TM %*% xx[,ii-1]
           }
       else {
        yr <- 4*plt
        A <- Q[yr,5:29]
        TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
```

```
      xx[,ii] <- TM %*% xx[,ii-1]
      }

   } #end of 40 gen. loop

   # Lambda calculated on seedbank at year 40
   lamda[repn*plt-(repn-1)+j-1,1] <- (xx[5,endtime])/(xx[5,endtime-1])
   lamda[repn*plt-(repn-1)+j-1,2] <- 1 #Label what environment

} #end of rep loop
}}#end of environment loop

#Environment 3: Meadow
else if (env >2)
if(env <=3){
for (plt in (pltnb+1):pltnc) #Change Number for which rows intial pop vector comes from in
data
{
 #Get the initial population vector
 xx0 <- matrix(as.numeric(IP[plt,5:9]), nrow=5, ncol=1, byrow=FALSE)

 for (j in 1:repn) {
  xx[,1] <- xx0
  for (ii in 2:endtime) {
   #Get a random uniform number between 0 and 1
   rv <- runif(1,min=0,max=1)
   #Associate the random number with one of the imported transition matrices (TM)
   # and multiply by the population vector from previous year xx[,ii-1] to create
   #a new pop. vector (xx0)
   if(rv <= .25) {
     #Get transition values from full data file and make transition matrix for yr
     yr <- 4*plt-3
     A <- Q[yr,5:29]
     TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
     xx[,ii] <- TM %*% xx[,ii-1]
     }
   else if(rv > .25)
     if(rv <= .5) {
       yr <- 4*plt-2
       A <- Q[yr,5:29]
       TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
       xx[,ii] <- TM %*% xx[,ii-1]
       }
```

```
     else if(rv > .5)
          if(rv <= .75) {
        yr <- 4*plt-1
        A <- Q[yr,5:29]
        TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
        xx[,ii] <- TM %*% xx[,ii-1]
        }
     else {
      yr <- 4*plt
      A <- Q[yr,5:29]
      TM <- matrix(as.numeric(A), nrow=5, ncol=5, byrow=FALSE)
      xx[,ii] <- TM %*% xx[,ii-1]
      }

   } #end of 40 gen. loop

   # Lambda calculated on seedbank at year 40
   lamda[repn*plt-(repn-1)+j-1,1] <- (xx[5,endtime])/(xx[5,endtime-1])
   lamda[repn*plt-(repn-1)+j-1,2] <- 3 #Label what environment

} #end of rep loop
}}}#end of environment loop

lamda #lambda matrix
#Boxplot of Lambda Distribution
boxplot(Lambda ~ Environment, data = lamda, names =
c("Burned","Burned and Salvage-logged","Meadow"),
ylim = c(0,10),ylab="Population Growth Rate")
abline(h=1,lty=5,col=2) #Change plot attributes
# creates a data file of the name "Lambda" in your working directory
write.table(lamda, file = "Lambda")
# Open with excel and use space delineated columns

###Step 2 ##########
###Prob of a Lambda > 1 #####################
#Matrix of 1 and 0 for if calculated lambda > 1
a=matrix(0,nrow=pltn*repn, ncol=2)
#Matrix for output
b=matrix(0,nrow=envn,ncol=4,dimnames = list(c("Burned",
"Burned & Salvage-logged","Meadow"),c("Sum","Prob > 1","Mean","StDev")))

#Envrioment 2: Burned and Salvage Logged
for (t in (1:(pltna*repn))){
```

```
a[t,2]=2} # insert environment number in matrix a

for (t in (1:(pltna*repn))){
if (lamda[t,1] > 1) # inserts 1 if lambda > 1
{
a[t,1]=1
}
#Calculating the Prob > 1, Mean Lambda, Stdev Lambda for enviroment 2
b[2,1]=sum(a[1:(pltna*repn),1],na.rm=FALSE) #Sum of 1's inserted if lambda > 1
b[2,2]=sum(a[1:(pltna*repn),1],na.rm=FALSE)/(pltna*repn) #Prob > 1
b[2,3]=mean(lamda[1:(pltna*repn),1],na.rm=FALSE) #Mean Lambda
b[2,4]=sqrt(var(lamda[1:(pltna*repn),1],na.rm=FALSE)) #Stdev Lambda
}

#Envrioment 1: Burned
for (t in ((pltna*repn)+1):((pltnbb*repn)+(pltna*repn))){
a[t,2]=1} # insert environment number in matrix a
for (t in ((pltna*repn)+1):((pltnbb*repn)+(pltna*repn))){
if (lamda[t,1] > 1) {
a[t,1]=1  # inserts 1 if lambda > 1
}
#Calculating the Prob > 1, Mean Lambda, Stdev Lambda for enviroment 1
b[1,1]=sum(a[((pltna*repn)+1):((pltnbb*repn)+(pltna*repn)),1],na.rm=FALSE)
#Sum of 1's inserted if lambda > 1
b[1,2]=sum(a[((pltna*repn)+1):((pltnbb*repn)+(pltna*repn)),1],na.rm=FALSE)/
(repn*pltnbb)#Prob >1
b[1,3]=mean(lamda[((pltna*repn)+1):((pltnbb*repn)+(pltna*repn)),1])
#Mean Lambda
b[1,4]=sqrt(var(lamda[((pltna*repn)+1):((pltnbb*repn)+(pltna*repn)),1]))
#Stdev Lambda
}

#Envrioment 3: Meadow
#for (t in (((pltnbb*repn)+(pltna*repn))+1):(repn*pltn)){
#a[t,2]=3} # insert environment number in matrix a
for (t in (((pltnbb*repn)+(pltna*repn))+1):(repn*pltn)){
if (lamda[t,1] > 1) {
a[t,1]=1  # inserts 1 if lambda > 1
}

#Calculating the Prob > 1, Mean Lambda, Stdev Lambda for enviroment 3
b[3,1]=sum(a[(((pltnbb*repn)+(pltna*repn))+1):(repn*pltn),1],na.rm=FALSE)
#Sum of 1's inserted if lambda > 1
```

```
b[3,2]=sum(a[(((pltnbb*repn)+(pltna*repn))+1):(repn*pltn),1],na.rm=FALSE)/
(repn*pltncc)#Prob >1
b[3,3]=mean(lamda[(((pltnbb*repn)+(pltna*repn))+1):(repn*pltn),1])#Mean Lambda
b[3,4]=sqrt(var(lamda[(((pltnbb*repn)+(pltna*repn))+1):(repn*pltn),1]))
#Stdev Lambda
}
b #Matrix b: the output matrixround(emat,4)
```

APPENDIX D

TRANSITION PARAMETER VALUES ACROSS ENVIRONMENTS

Table D.1. Mean (± standard deviation) for each transition from 2001.

	Mean transition values(2001)[a]										
Sites[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.805	0.838	0.149	0.010	0.715	1005	0.775	0.053	0.276	0.017	0.715
n = 40	(0.297)	(0.205)	(0.188)	(0.015)	(0.142)	(631)	(0.223)	(0.179)	(0.333)	(0.333)	(0.142)
B	0.758	0.826	0.166	0.003	0.720	1202	0.806	0.033	0.255	0.014	0.720
n = 50	(0.371)	(0.221)	(0.225)	(0.006)	(0.720)	(1305)	(0.255)	(0.152)	(0.412)	(0.029)	(0.720)
M	0.100	0.743	0.257	0.000	0.880	2705	0.871	0.000	0.000	0.001	0.880
n = 5	(0.224)	(0.183)	(0.183)	(0.000)	(*)	(1512)	(0.217)	(0.000)	(0.000)	(0.001)	(*)

Table D.2. Mean (± standard deviation) for each transition from 2002.

	Mean transition values(2002)[a]										
Sites[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.657	0.850	0.037	0.001	0.715	1134	0.420	0.056	0.050	0.024	0.715
n = 40	(0.321)	(0.174)	(0.073)	(0.002)	(0.142)	(1582)	(0.270)	(0.154)	(0.221)	(0.221)	(0.142)
B	0.532	0.708	0.115	0.000	0.720	973	0.451	0.017	0.000	0.019	0.720
n = 50	(0.408)	(0.282)	(0.220)	(0.000)	(0.720)	(1094)	(0.327)	(0.084)	(0.000)	(0.030)	(0.720)
M	0.450	0.767	0.000	0.000	0.880	0.000	0.233	0.000	0.000	0.000	0.880
n = 5	(0.447)	(0.435)	(0.000)	(0.000)	(*)	(0.000)	(0.325)	(0.000)	(0.000)	(0.000)	(*)

Table D.3. Mean (± standard deviation) for each transition from 2003.

	Mean transition values(2003)[a]										
Sites[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.378	0.703	0.033	0.003	0.715	3009	0.623	0.093	0.386	0.015	0.715
n = 40	(0.397)	(0.299)	(0.070)	(0.007)	(0.142)	(2734)	(0243)	(0.249)	(0.366)	(0.366)	(0.142)
B	0.347	0.584	0.095	0.002	0.720	1271	0.636	0.000	0.273	0.004	0.720
n = 50	(0.418)	(0.362)	(0.221)	(0.005)	(0.720)	(1465)	(0.319)	(0.000)	(0.359)	(0.008)	(0.720)
M	0.000	0.200	0.000	0.000	0.880	1825	0.367	0.000	0.000	0.000	0.880
n = 5	(0.000)	(0.447)	(0.000)	(0.000)	(*)	(4080)	(0.415)	(0.000)	(0.000)	(0.000)	(*)

Table D.4. Mean (± standard deviation) for each transition from 2004.

	Mean transition values(2004)[a]										
Sites[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.677	0.797	0.051	0.046	0.715	2537	0.623	0.093	0.386	0.015	0.715
n = 40	(0.326)	(0.227)	(0.072)	88)00	(0.142)	(2058)	(0.243)	(0.249)	(0.366)	(0.366)	(0.142)
B	0.519	0.726	0.020	0.010	0.720	1410	0.631	0.000	0.273	0.004	0.720
n = 50	(0.410)	(0.294)	(0.043)	(0.021)	(0.720)	(1699)	(0.310)	(0.000)	(0.359)	(0.008)	(0.720)
M	0.462	0.896	0.000	0.000	0.880	1825	0.367	0.000	0.000	0.000	0.880
n = 5	(0.434)	(0.137)	(0.000)	(0.000)	(*)	(4080)	(0.415)	(0.00)	(0.000)	(0.000)	(*)

Table D.5. Mean (± standard deviation) for each transition from 2005.

	Mean transition values(2005)[a]										
Sites[b]	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL	0.387	0.699	0.071	0.002	0.715	934	0.605	0.113	0.316	0.001	0.715
n = 40	(0.343)	(0.248)	(0.138)	(0.004)	(0.142)	(1181)	(0.243)	(0.212)	(0.335)	(0.335)	(0.142)
B	0.403	0.655	0.028	0.002	0.720	658	0.626	0.062	0.264	0.001	0.720
n = 50	(0.448)	(0.342)	(0.053)	(0.009)	(0.720)	(1131)	(0.328)	(0.181)	(0.285)	(0.002)	(0.720)
M	0.000	0.180	0.000	0.000	0.880	0 (0)	0.000	0.000	0.000	0.000	0.880
n = 5	(0.000)	(0.249)	(0.000)	(0.000)	(*)		(0.000)	(0.000)	(0.000)	(0.000)	(*)

Table D.6. Transition rates for each environment for fall to fall from 2001 through 2005 (see A.2 for transition definitions).

Environment	Transect	Plot	Transition	2002	2003	2004	2005
Burned and Salvage-logged	1	1	T1	0.010	0.010	0.000	0.000
Burned and Salvage-logged	1	1	T2	1.000	1.000	1.000	0.278
Burned and Salvage-logged	1	1	T3	1.000	0.855	0.936	0.341
Burned and Salvage-logged	1	1	T4	0.300	0.000	0.000	0.000
Burned and Salvage-logged	1	1	T5	0.089	0.073	0.000	0.000
Burned and Salvage-logged	1	1	T6	1362.000	1506.000	0.000	0.000
Burned and Salvage-logged	1	1	T8	0.923	0.819	0.645	0.684
Burned and Salvage-logged	1	2	T1	0.010	0.010	0.060	0.000
Burned and Salvage-logged	1	2	T2	1.000	1.000	1.000	0.128
Burned and Salvage-logged	1	2	T3	0.873	0.882	0.402	0.487
Burned and Salvage-logged	1	2	T4	0.000	0.500	0.500	0.000
Burned and Salvage-logged	1	2	T5	0.016	0.018	0.010	0.000
Burned and Salvage-logged	1	2	T6	1362.000	2477.000	5776.000	0.000
Burned and Salvage-logged	1	2	T8	0.861	0.913	0.994	0.683
Burned and Salvage-logged	1	3	T1	0.010	0.030	0.220	0.006
Burned and Salvage-logged	1	3	T2	1.000	1.000	1.000	0.273
Burned and Salvage-logged	1	3	T3	0.884	0.676	0.939	1.000
Burned and Salvage-logged	1	3	T4	0.250	1.000	1.000	0.333
Burned and Salvage-logged	1	3	T5	0.024	0.014	0.061	0.076
Burned and Salvage-logged	1	3	T6	1362.000	1858.000	5776.000	14231.000
Burned and Salvage-logged	1	3	T8	0.595	0.669	0.650	0.473
Burned and Salvage-logged	1	4	T1	0.000	0.030	0.100	0.002
Burned and Salvage-logged	1	4	T2	1.000	0.000	1.000	0.520
Burned and Salvage-logged	1	4	T3	1.000	0.625	0.819	0.756
Burned and Salvage-logged	1	4	T4	0.714	0.667	0.000	0.000
Burned and Salvage-logged	1	4	T5	0.019	0.006	0.029	0.035
Burned and Salvage-logged	1	4	T6	1362.000	2101.000	2888.000	6099.000
Burned and Salvage-logged	1	4	T8	0.531	0.739	0.811	0.580
Burned and Salvage-logged	1	5	T1	0.000	0.030	0.000	0.000
Burned and Salvage-logged	1	5	T2	1.000	0.000	1.000	0.671
Burned and Salvage-logged	1	5	T3	1.000	0.553	1.000	0.815
Burned and Salvage-logged	1	5	T4	0.250	0.500	0.000	0.200
Burned and Salvage-logged	1	5	T5	0.023	0.000	0.079	0.000
Burned and Salvage-logged	1	5	T6	1362.000	2101.000	0.000	0.000
Burned and Salvage-logged	1	5	T8	0.739	0.770	0.713	0.606

Burned and Salvage-logged	1	6	T1	0.000	0.000	0.030	0.000
Burned and Salvage-logged	1	6	T2	1.000	0.000	1.000	0.249
Burned and Salvage-logged	1	6	T3	1.000	0.620	1.000	0.459
Burned and Salvage-logged	1	6	T4	1.000	0.667	0.200	0.333
Burned and Salvage-logged	1	6	T5	0.063	0.063	0.061	0.071
Burned and Salvage-logged	1	6	T6	1362.000	2272.000	14440.000	14231.000
Burned and Salvage-logged	1	6	T8	0.739	0.438	0.693	0.873
Burned and Salvage-logged	1	7	T1	0.000	0.010	0.010	0.009
Burned and Salvage-logged	1	7	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	1	7	T3	1.000	0.765	0.832	0.774
Burned and Salvage-logged	1	7	T4	0.125	0.250	0.250	0.000
Burned and Salvage-logged	1	7	T5	0.069	0.030	0.000	0.012
Burned and Salvage-logged	1	7	T6	1362.000	2101.000	5776.000	2033.000
Burned and Salvage-logged	1	7	T8	0.752	0.911	0.701	0.861
Burned and Salvage-logged	1	8	T1	0.000	0.000	0.050	0.003
Burned and Salvage-logged	1	8	T2	1.000	0.000	1.000	1.000
Burned and Salvage-logged	1	8	T3	1.000	0.282	1.000	0.528
Burned and Salvage-logged	1	8	T4	1.000	0.000	1.000	0.000
Burned and Salvage-logged	1	8	T5	0.000	0.004	0.000	0.035
Burned and Salvage-logged	1	8	T6	1362.000	0.000	2888.000	10165.000
Burned and Salvage-logged	1	8	T8	0.791	0.826	0.711	0.653
Burned and Salvage-logged	1	9	T1	0.010	0.010	0.140	0.027
Burned and Salvage-logged	1	9	T2	1.000	1.000	1.000	0.113
Burned and Salvage-logged	1	9	T3	1.000	0.688	0.880	0.848
Burned and Salvage-logged	1	9	T4	0.177	0.714	0.000	0.231
Burned and Salvage-logged	1	9	T5	0.219	0.028	0.173	0.106
Burned and Salvage-logged	1	9	T6	1362.000	2392.000	8664.000	12198.000
Burned and Salvage-logged	1	9	T8	0.920	0.739	0.725	0.810
Burned and Salvage-logged	1	10	T1	0.010	0.000	0.020	0.008
Burned and Salvage-logged	1	10	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	1	10	T3	1.000	0.673	0.865	1.000
Burned and Salvage-logged	1	10	T4	0.632	0.300	1.000	0.000
Burned and Salvage-logged	1	10	T5	0.345	0.018	0.081	0.125
Burned and Salvage-logged	1	10	T6	1362.000	2101.000	2888.000	8132.000
Burned and Salvage-logged	1	10	T8	0.587	0.968	0.729	0.658
Burned and Salvage-logged	3	1	T1	0.040	0.010	0.000	0.000
Burned and Salvage-logged	3	1	T2	1.000	1.000	1.000	0.308
Burned and Salvage-logged	3	1	T3	0.771	0.741	0.900	0.556
Burned and Salvage-logged	3	1	T4	0.000	0.500	0.000	0.000
Burned and Salvage-logged	3	1	T5	0.029	0.000	0.050	0.000
Burned and Salvage-logged	3	1	T6	1143.000	2046.000	0.000	0.000
Burned and Salvage-logged	3	1	T8	0.910	0.739	0.666	0.968
Burned and Salvage-logged	3	2	T1	0.010	0.000	0.000	0.000
Burned and Salvage-logged	3	2	T2	0.000	1.000	1.000	1.000
Burned and Salvage-logged	3	2	T3	0.914	0.469	1.000	0.818
Burned and Salvage-logged	3	2	T4	0.667	0.000	0.000	0.000
Burned and Salvage-logged	3	2	T5	0.000	0.000	0.200	0.000
Burned and Salvage-logged	3	2	T6	1143.000	0.000	0.000	1792.000
Burned and Salvage-logged	3	2	T8	0.716	0.664	0.739	0.790

Burned and Salvage-logged	3	3	T1	0.010	0.000	0.000	0.000
Burned and Salvage-logged	3	3	T2	1.000	1.000	1.000	0.833
Burned and Salvage-logged	3	3	T3	0.750	0.424	0.786	0.909
Burned and Salvage-logged	3	3	T4	0.333	0.000	0.000	0.000
Burned and Salvage-logged	3	3	T5	0.000	0.000	0.071	0.000
Burned and Salvage-logged	3	3	T6	1143.000	0.000	0.000	0.000
Burned and Salvage-logged	3	3	T8	0.459	0.830	0.637	0.739
Burned and Salvage-logged	3	4	T1	0.010	0.000	0.000	0.000
Burned and Salvage-logged	3	4	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	3	4	T3	0.662	0.449	1.000	1.000
Burned and Salvage-logged	3	4	T4	0.000	0.000	0.000	1.000
Burned and Salvage-logged	3	4	T5	0.000	0.000	0.046	0.000
Burned and Salvage-logged	3	4	T6	1143.000	0.000	0.000	0.000
Burned and Salvage-logged	3	4	T8	0.909	0.739	0.698	0.803
Burned and Salvage-logged	3	5	T1	0.030	0.000	0.000	0.000
Burned and Salvage-logged	3	5	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	3	5	T3	1.000	0.701	1.000	0.745
Burned and Salvage-logged	3	5	T4	0.625	0.000	0.000	0.500
Burned and Salvage-logged	3	5	T5	0.016	0.000	0.037	0.000
Burned and Salvage-logged	3	5	T6	299.000	1678.000	0.000	0.000
Burned and Salvage-logged	3	5	T8	0.442	0.912	0.672	0.713
Burned and Salvage-logged	3	6	T1	0.010	0.010	0.000	0.000
Burned and Salvage-logged	3	6	T2	0.000	1.000	1.000	1.000
Burned and Salvage-logged	3	6	T3	0.978	0.539	0.833	0.750
Burned and Salvage-logged	3	6	T4	1.000	0.000	0.000	0.000
Burned and Salvage-logged	3	6	T5	0.011	0.000	0.000	0.000
Burned and Salvage-logged	3	6	T6	675.000	1381.000	0.000	0.000
Burned and Salvage-logged	3	6	T8	0.891	0.584	0.683	0.551
Burned and Salvage-logged	3	7	T1	0.010	0.010	0.080	0.000
Burned and Salvage-logged	3	7	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	3	7	T3	1.000	0.600	0.667	0.708
Burned and Salvage-logged	3	7	T4	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	7	T5	0.019	0.000	0.000	0.000
Burned and Salvage-logged	3	7	T6	1143.000	1381.000	2548.000	0.000
Burned and Salvage-logged	3	7	T8	0.701	0.739	0.781	0.637
Burned and Salvage-logged	3	8	T1	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	8	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	3	8	T3	1.000	0.678	0.818	0.815
Burned and Salvage-logged	3	8	T4	0.667	0.000	0.000	0.000
Burned and Salvage-logged	3	8	T5	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	8	T6	1143.000	0.000	0.000	0.000
Burned and Salvage-logged	3	8	T8	0.707	0.682	0.960	0.918
Burned and Salvage-logged	3	9	T1	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	9	T2	1.000	1.000	1.000	1.000
Burned and Salvage-logged	3	9	T3	0.811	0.452	0.515	0.529
Burned and Salvage-logged	3	9	T4	1.000	0.000	0.000	0.000
Burned and Salvage-logged	3	9	T5	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	9	T6	1143.000	0.000	0.000	0.000
Burned and Salvage-logged	3	9	T8	0.810	0.653	0.723	0.789

Burned and Salvage-logged	3	10	T1	0.000	0.060	0.000	0.000
Burned and Salvage-logged	3	10	T2	0.000	1.000	1.000	1.000
Burned and Salvage-logged	3	10	T3	1.000	0.663	0.627	0.524
Burned and Salvage-logged	3	10	T4	0.000	0.000	0.000	0.000
Burned and Salvage-logged	3	10	T5	0.012	0.000	0.000	0.000
Burned and Salvage-logged	3	10	T6	2456.000	420.000	0.000	8960.000
Burned and Salvage-logged	3	10	T8	0.923	0.539	0.584	0.606
Burned and Salvage-logged	6	1	T1	0.000			0.000
Burned and Salvage-logged	6	1	T2	0.000			0.000
Burned and Salvage-logged	6	1	T3	1.000			1.000
Burned and Salvage-logged	6	1	T4	0.000			0.250
Burned and Salvage-logged	6	1	T5	0.133			0.333
Burned and Salvage-logged	6	1	T6	1421.000			5205.000
Burned and Salvage-logged	6	1	T8	0.580			0.857
Burned and Salvage-logged	6	2	T1	0.000			0.001
Burned and Salvage-logged	6	2	T2	1.000			1.000
Burned and Salvage-logged	6	2	T3	1.000			0.660
Burned and Salvage-logged	6	2	T4	0.000			0.000
Burned and Salvage-logged	6	2	T5	0.100			0.040
Burned and Salvage-logged	6	2	T6	1421.000			3470.000
Burned and Salvage-logged	6	3	T8	0.707			0.526
Burned and Salvage-logged	6	3	T1	0.000			0.006
Burned and Salvage-logged	6	3	T2	1.000			1.000
Burned and Salvage-logged	6	3	T3	1.000			0.352
Burned and Salvage-logged	6	3	T4	0.000			0.000
Burned and Salvage-logged	6	3	T5	0.000			0.014
Burned and Salvage-logged	6	3	T6	1421.000			1735.000
Burned and Salvage-logged	6	3	T8	0.741			0.832
Burned and Salvage-logged	6	4	T1	0.010			0.001
Burned and Salvage-logged	6	4	T2	1.000			1.000
Burned and Salvage-logged	6	4	T3	1.000			0.533
Burned and Salvage-logged	6	4	T4	0.125			0.125
Burned and Salvage-logged	6	4	T5	0.025			0.066
Burned and Salvage-logged	6	4	T6	1634.889			13880.000
Burned and Salvage-logged	6	4	T8	0.931			0.782
Burned and Salvage-logged	6	5	T1	0.000			0.000
Burned and Salvage-logged	6	5	T2	0.000			0.000
Burned and Salvage-logged	6	5	T3	0.927			0.049
Burned and Salvage-logged	6	5	T4	0.333			0.000
Burned and Salvage-logged	6	5	T5	0.098			0.000
Burned and Salvage-logged	6	5	T6	1421.000			0.000
Burned and Salvage-logged	6	5	T8	0.872			0.709
Burned and Salvage-logged	6	6	T1	0.000			0.000
Burned and Salvage-logged	6	6	T2	1.000			1.000
Burned and Salvage-logged	6	6	T3	0.976			0.265
Burned and Salvage-logged	6	6	T4	0.333			0.000
Burned and Salvage-logged	6	6	T5	0.000			0.036
Burned and Salvage-logged	6	6	T6	1421.000			5205.000
Burned and Salvage-logged	6	6	T8	0.659			0.816

Burned and Salvage-logged	6	7	T1	0.000	0.000
Burned and Salvage-logged	6	7	T2	1.000	1.000
Burned and Salvage-logged	6	7	T3	0.172	0.172
Burned and Salvage-logged	6	7	T4	0.000	0.000
Burned and Salvage-logged	6	7	T5	0.000	0.000
Burned and Salvage-logged	6	7	T6	1421.000	0.000
Burned and Salvage-logged	6	7	T8	0.974	0.855
Burned and Salvage-logged	6	8	T1	0.000	0.001
Burned and Salvage-logged	6	8	T2	0.000	0.000
Burned and Salvage-logged	6	8	T3	1.000	1.000
Burned and Salvage-logged	6	8	T4	1.000	0.000
Burned and Salvage-logged	6	8	T5	0.250	0.250
Burned and Salvage-logged	6	8	T6	1421.000	1735.000
Burned and Salvage-logged	6	8	T8	0.804	0.714
Burned and Salvage-logged	6	9	T1	0.000	0.000
Burned and Salvage-logged	6	9	T2	0.000	0.000
Burned and Salvage-logged	6	9	T3	1.000	0.333
Burned and Salvage-logged	6	9	T4	1.000	0.000
Burned and Salvage-logged	6	9	T5	0.000	0.000
Burned and Salvage-logged	6	9	T6	1421.000	0.000
Burned and Salvage-logged	6	9	T8	0.994	0.848
Burned and Salvage-logged	6	10	T1	0.010	0.001
Burned and Salvage-logged	6	10	T2	1.000	1.000
Burned and Salvage-logged	6	10	T3	1.000	0.290
Burned and Salvage-logged	6	10	T4	0.333	0.000
Burned and Salvage-logged	6	10	T5	0.000	0.258
Burned and Salvage-logged	6	10	T6	459.000	17350.000
Burned and Salvage-logged	6	10	T8	0.836	0.497
Burned and Salvage-logged	9	1	T1	0.000	0.028
Burned and Salvage-logged	9	1	T2	1.000	1.000
Burned and Salvage-logged	9	1	T3	0.937	1.000
Burned and Salvage-logged	9	1	T4	0.000	0.000
Burned and Salvage-logged	9	1	T5	0.000	0.009
Burned and Salvage-logged	9	1	T6	1362.000	2222.000
Burned and Salvage-logged	9	1	T8	0.732	0.543
Burned and Salvage-logged	9	2	T1	0.000	0.000
Burned and Salvage-logged	9	2	T2	0.000	0.000
Burned and Salvage-logged	9	2	T3	0.732	0.393
Burned and Salvage-logged	9	2	T4	0.000	0.000
Burned and Salvage-logged	9	2	T5	0.000	0.000
Burned and Salvage-logged	9	2	T6	1362.000	0.000
Burned and Salvage-logged	9	2	T8	0.616	0.627
Burned and Salvage-logged	9	3	T1	0.000	0.000
Burned and Salvage-logged	9	3	T2	1.000	1.000
Burned and Salvage-logged	9	3	T3	0.905	0.524
Burned and Salvage-logged	9	3	T4	0.000	0.000
Burned and Salvage-logged	9	3	T5	0.000	0.095
Burned and Salvage-logged	9	3	T6	1362.000	4444.000
Burned and Salvage-logged	9	3	T8	0.759	0.883

Burned and Salvage-logged	9	4	T1	0.000	0.000
Burned and Salvage-logged	9	4	T2	0.000	0.000
Burned and Salvage-logged	9	4	T3	1.000	0.333
Burned and Salvage-logged	9	4	T4	0.250	0.000
Burned and Salvage-logged	9	4	T5	0.000	0.000
Burned and Salvage-logged	9	4	T6	1362.000	0.000
Burned and Salvage-logged	9	4	T8	0.897	0.704
Burned and Salvage-logged	9	5	T1	0.000	0.000
Burned and Salvage-logged	9	5	T2	0.000	0.000
Burned and Salvage-logged	9	5	T3	1.000	0.500
Burned and Salvage-logged	9	5	T4	0.000	0.000
Burned and Salvage-logged	9	5	T5	0.000	0.250
Burned and Salvage-logged	9	5	T6	1362.000	2222.000
Burned and Salvage-logged	9	5	T8	0.968	0.754
Burned and Salvage-logged	9	6	T1	0.000	0.007
Burned and Salvage-logged	9	6	T2	1.000	1.000
Burned and Salvage-logged	9	6	T3	0.982	0.611
Burned and Salvage-logged	9	6	T4	0.000	0.000
Burned and Salvage-logged	9	6	T5	0.019	0.037
Burned and Salvage-logged	9	6	T6	1362.000	4444.000
Burned and Salvage-logged	9	6	T8	0.498	0.653
Burned and Salvage-logged	9	7	T1	0.000	0.000
Burned and Salvage-logged	9	7	T2	0.000	0.000
Burned and Salvage-logged	9	7	T3	1.000	0.400
Burned and Salvage-logged	9	7	T4	0.000	0.000
Burned and Salvage-logged	9	7	T5	0.000	0.000
Burned and Salvage-logged	9	7	T6	1362.000	0.000
Burned and Salvage-logged	9	7	T8	0.604	0.725
Burned and Salvage-logged	9	8	T1	0.000	0.000
Burned and Salvage-logged	9	8	T2	0.000	0.000
Burned and Salvage-logged	9	8	T3	1.000	1.000
Burned and Salvage-logged	9	8	T4	0.000	0.000
Burned and Salvage-logged	9	8	T5	0.000	0.000
Burned and Salvage-logged	9	8	T6	1362.000	0.000
Burned and Salvage-logged	9	8	T8	0.634	0.805
Burned and Salvage-logged	9	9	T1	0.000	0.000
Burned and Salvage-logged	9	9	T2	0.000	0.000
Burned and Salvage-logged	9	9	T3	0.000	0.000
Burned and Salvage-logged	9	9	T4	0.500	0.000
Burned and Salvage-logged	9	9	T5	0.000	0.000
Burned and Salvage-logged	9	9	T6	1362.000	0.000
Burned and Salvage-logged	9	9	T8	0.846	0.669
Burned and Salvage-logged	9	10	T1	0.000	0.000
Burned and Salvage-logged	9	10	T2	0.000	0.000
Burned and Salvage-logged	9	10	T3	0.750	1.000
Burned and Salvage-logged	9	10	T4	0.000	0.000
Burned and Salvage-logged	9	10	T5	0.500	0.500
Burned and Salvage-logged	9	10	T6	1362.000	0.000
Burned and Salvage-logged	9	10	T8	0.835	0.739

Burned	2	1	T1	0.030	0.030	0.000	0.000
Burned	2	1	T2	1.000	1.000	1.000	0.500
Burned	2	1	T3	1.000	0.875	0.500	1.000
Burned	2	1	T4	0.200	0.000	0.000	0.000
Burned	2	1	T5	0.076	0.000	0.014	0.000
Burned	2	1	T6	916.500	954.000	0.000	0.000
Burned	2	1	T8	0.614	0.820	0.918	0.369
Burned	2	2	T1	0.060	0.010	0.050	0.001
Burned	2	2	T2	1.000	1.000	1.000	0.722
Burned	2	2	T3	1.000	0.444	0.900	0.371
Burned	2	2	T4	1.000	0.667	0.000	0.000
Burned	2	2	T5	0.041	0.022	0.000	0.029
Burned	2	2	T6	434.000	1206.000	3948.000	1937.000
Burned	2	2	T8	0.893	0.659	0.784	0.362
Burned	2	3	T1	0.050	0.050	0.000	0.000
Burned	2	3	T2	1.000	1.000	1.000	0.675
Burned	2	3	T3	1.000	0.680	0.774	0.750
Burned	2	3	T4	0.000	0.000	0.000	0.000
Burned	2	3	T5	0.015	0.000	0.000	0.083
Burned	2	3	T6	662.000	856.000	0.000	5811.000
Burned	2	3	T8	1.000	0.476	0.913	0.535
Burned	2	4	T1	0.000	0.000	0.000	0.001
Burned	2	4	T2	0.000	1.000	1.000	0.897
Burned	2	4	T3	1.000	0.517	1.000	0.634
Burned	2	4	T4	0.714	0.000	0.000	0.000
Burned	2	4	T5	0.000	0.000	0.000	0.122
Burned	2	4	T6	693.000	0.000	0.000	9685.000
Burned	2	4	T8	0.561	0.500	0.660	0.596
Burned	2	5	T1	0.010	0.000	0.000	0.000
Burned	2	5	T2	0.000	1.000	1.000	1.000
Burned	2	5	T3	1.000	0.943	1.000	0.650
Burned	2	5	T4	0.333	0.000	0.000	0.000
Burned	2	5	T5	0.000	0.000	0.121	0.050
Burned	2	5	T6	693.000	0.000	0.000	1937.000
Burned	2	5	T8	0.820	0.597	0.496	0.811
Burned	2	6	T1	0.000	0.000	0.000	0.000
Burned	2	6	T2	0.000	0.000	0.833	1.000
Burned	2	6	T3	0.500	0.875	0.714	0.545
Burned	2	6	T4	0.000	0.000	0.000	0.000
Burned	2	6	T5	0.000	0.000	0.000	0.061
Burned	2	6	T6	693.000	0.000	0.000	7748.000
Burned	2	6	T8	0.719	0.552	0.849	0.556
Burned	2	7	T1	0.020	0.000	0.000	0.000
Burned	2	7	T2	0.000	1.000	1.000	1.000
Burned	2	7	T3	1.000	0.575	0.960	0.600
Burned	2	7	T4	0.333	0.000	0.000	0.000
Burned	2	7	T5	0.000	0.000	0.000	0.000
Burned	2	7	T6	613.500	0.000	0.000	0.000
Burned	2	7	T8	0.648	0.636	0.294	0.797

Burned	2	8	T1	0.000	0.010	0.000	0.000
Burned	2	8	T2	0.000	1.000	1.000	1.000
Burned	2	8	T3	0.833	0.700	1.000	0.729
Burned	2	8	T4	0.000	0.000	0.000	0.000
Burned	2	8	T5	0.083	0.000	0.000	0.000
Burned	2	8	T6	693.000	407.000	0.000	0.000
Burned	2	8	T8	0.915	0.820	0.506	0.704
Burned	2	9	T1	0.020	0.000	0.000	0.000
Burned	2	9	T2	1.000	1.000	1.000	1.000
Burned	2	9	T3	1.000	0.600	0.500	1.000
Burned	2	9	T4	0.000	0.000	0.000	0.000
Burned	2	9	T5	0.000	0.000	0.000	0.000
Burned	2	9	T6	693.000	0.000	0.000	0.000
Burned	2	9	T8	0.579	0.373	0.613	0.851
Burned	2	10	T1	0.000	0.000	0.000	0.000
Burned	2	10	T2	0.000	1.000	0.500	0.250
Burned	2	10	T3	0.533	0.375	0.333	0.333
Burned	2	10	T4	0.000	0.000	0.000	0.000
Burned	2	10	T5	0.000	0.000	0.000	0.000
Burned	2	10	T6	693.000	0.000	0.000	0.000
Burned	2	10	T8	0.590	0.820	0.173	0.938
Burned	4	1	T1	0.020	0.000	0.000	0.000
Burned	4	1	T2	1.000	1.000	1.000	0.015
Burned	4	1	T3	1.000	0.741	0.900	0.028
Burned	4	1	T4	0.000	0.500	0.000	0.000
Burned	4	1	T5	0.500	0.000	0.050	0.000
Burned	4	1	T6	2928.600	0.000	0.000	0.000
Burned	4	1	T8	0.920	0.668	0.474	0.820
Burned	4	2	T1	0.000	0.000	0.000	0.000
Burned	4	2	T2	1.000	1.000	1.000	1.000
Burned	4	2	T3	1.000	0.469	1.000	0.545
Burned	4	2	T4	0.667	0.000	0.000	0.000
Burned	4	2	T5	0.000	0.000	0.200	0.000
Burned	4	2	T6	2928.600	0.000	0.000	0.000
Burned	4	2	T8	0.820	0.971	0.820	0.820
Burned	4	3	T1	0.000	0.010	0.010	0.000
Burned	4	3	T2	0.000	1.000	1.000	1.000
Burned	4	3	T3	1.000	0.424	0.786	1.000
Burned	4	3	T4	0.143	0.000	0.000	1.000
Burned	4	3	T5	0.000	0.000	0.071	0.000
Burned	4	3	T6	2928.600	2115.000	2996.000	0.000
Burned	4	3	T8	0.679	0.330	0.555	0.978
Burned	4	4	T1	0.000	0.010	0.000	0.000
Burned	4	4	T2	1.000	1.000	1.000	0.179
Burned	4	4	T3	1.000	0.449	1.000	0.172
Burned	4	4	T4	0.000	0.000	0.000	0.000
Burned	4	4	T5	0.000	0.000	0.046	0.000
Burned	4	4	T6	2244.000	3191.000	0.000	0.000
Burned	4	4	T8	0.472	0.820	0.731	0.820

Burned	4	5	T1	0.000	0.000	0.000	0.006
Burned	4	5	T2	1.000	1.000	1.000	1.000
Burned	4	5	T3	1.000	0.701	1.000	0.782
Burned	4	5	T4	0.417	0.000	0.000	0.000
Burned	4	5	T5	0.016	0.000	0.037	0.018
Burned	4	5	T6	5549.000	2453.000	0.000	1429.000
Burned	4	5	T8	0.801	0.820	0.686	0.643
Burned	4	6	T1	0.000	0.010	0.000	0.000
Burned	4	6	T2	1.000	1.000	1.000	1.000
Burned	4	6	T3	1.000	0.539	0.833	0.500
Burned	4	6	T4	0.143	0.000	0.000	0.000
Burned	4	6	T5	0.020	0.000	0.000	0.000
Burned	4	6	T6	3395.000	2453.000	0.000	0.000
Burned	4	6	T8	0.820	0.931	0.820	0.161
Burned	4	7	T1	0.010	0.000	0.000	0.000
Burned	4	7	T2	1.000	1.000	1.000	0.857
Burned	4	7	T3	1.000	0.600	0.667	0.500
Burned	4	7	T4	0.000	0.000	0.000	0.000
Burned	4	7	T5	0.024	0.000	0.000	0.000
Burned	4	7	T6	1211.000	0.000	0.000	0.000
Burned	4	7	T8	0.802	0.811	0.820	0.365
Burned	4	8	T1	0.000	0.010	0.000	0.002
Burned	4	8	T2	0.000	1.000	1.000	0.260
Burned	4	8	T3	1.000	0.678	0.818	0.160
Burned	4	8	T4	1.000	0.000	0.000	0.000
Burned	4	8	T5	0.000	0.000	0.000	0.012
Burned	4	8	T6	2929.000	2453.000	0.000	1429.000
Burned	4	8	T8	0.396	0.833	0.794	0.870
Burned	4	9	T1	0.000	0.020	0.000	0.003
Burned	4	9	T2	1.000	1.000	1.000	1.000
Burned	4	9	T3	1.000	0.452	0.515	1.000
Burned	4	9	T4	0.250	0.000	0.000	0.000
Burned	4	9	T5	0.000	0.000	0.000	0.059
Burned	4	9	T6	2929.000	2054.000	0.000	1429.000
Burned	4	9	T8	0.636	0.678	0.481	0.416
Burned	4	10	T1	0.000	0.000	0.000	0.002
Burned	4	10	T2	0.000	1.000	1.000	1.000
Burned	4	10	T3	1.000	0.663	0.627	0.667
Burned	4	10	T4	0.000	0.000	0.000	0.000
Burned	4	10	T5	0.022	0.000	0.000	0.071
Burned	4	10	T6	2929.000	0.000	0.000	1429.000
Burned	4	10	T8	0.849	0.779	0.299	0.820
Burned	7	1	T1	0.000			0.000
Burned	7	1	T2	0.000			0.000
Burned	7	1	T3	0.500			1.000
Burned	7	1	T4	0.000			0.000
Burned	7	1	T5	1.000			0.000
Burned	7	1	T6	2073.000			2699.000
Burned	7	1	T8	0.746			0.880

Burned	7	2	T1	0.000	0.001
Burned	7	2	T2	1.000	1.000
Burned	7	2	T3	1.000	0.949
Burned	7	2	T4	0.000	0.000
Burned	7	2	T5	0.051	0.051
Burned	7	2	T6	2333.000	5398.000
Burned	7	2	T8	0.664	0.871
Burned	7	3	T1	0.000	0.070
Burned	7	3	T2	0.000	0.000
Burned	7	3	T3	0.786	1.000
Burned	7	3	T4	0.250	0.000
Burned	7	3	T5	0.429	0.143
Burned	7	3	T6	2073.000	2699.000
Burned	7	3	T8	0.820	0.698
Burned	7	4	T1	0.000	0.000
Burned	7	4	T2	1.000	1.000
Burned	7	4	T3	1.000	1.000
Burned	7	4	T4	0.000	0.000
Burned	7	4	T5	0.083	0.667
Burned	7	4	T6	2073.000	21592.000
Burned	7	4	T8	0.757	0.364
Burned	7	5	T1	0.000	0.000
Burned	7	5	T2	1.000	1.000
Burned	7	5	T3	0.815	0.074
Burned	7	5	T4	0.000	0.000
Burned	7	5	T5	0.037	0.000
Burned	7	5	T6	2073.000	0.000
Burned	7	5	T8	0.820	0.820
Burned	7	6	T1	0.000	0.000
Burned	7	6	T2	0.000	0.000
Burned	7	6	T3	0.862	0.431
Burned	7	6	T4	0.000	0.000
Burned	7	6	T5	0.035	0.000
Burned	7	6	T6	1900.300	0.000
Burned	7	6	T8	0.820	0.573
Burned	7	7	T1	0.010	0.000
Burned	7	7	T2	0.000	0.000
Burned	7	7	T3	0.000	0.000
Burned	7	7	T4	0.000	0.000
Burned	7	7	T5	0.000	0.000
Burned	7	7	T6	2073.000	0.000
Burned	7	7	T8	0.820	0.557
Burned	7	8	T1	0.000	0.000
Burned	7	8	T2	1.000	1.000
Burned	7	8	T3	1.000	0.667
Burned	7	8	T4	0.000	0.000
Burned	7	8	T5	0.000	0.000
Burned	7	8	T6	2073.000	0.000
Burned	7	8	T8	0.940	0.495

Burned	7	9	T1	0.010	0.000
Burned	7	9	T2	0.000	0.000
Burned	7	9	T3	0.920	0.000
Burned	7	9	T4	0.000	0.000
Burned	7	9	T5	0.000	0.000
Burned	7	9	T6	2073.000	0.000
Burned	7	9	T8	0.820	0.383
Burned	7	10	T1	0.000	0.003
Burned	7	10	T2	1.000	1.000
Burned	7	10	T3	1.000	0.382
Burned	7	10	T4	0.000	0.000
Burned	7	10	T5	0.000	0.029
Burned	7	10	T6	2073.000	2699.000
Burned	7	10	T8	0.638	0.820
Burned	8	1	T1	0.000	0.000
Burned	8	1	T2	1.000	1.000
Burned	8	1	T3	0.955	0.409
Burned	8	1	T4	0.000	0.000
Burned	8	1	T5	0.000	0.000
Burned	8	1	T6	1180.000	0.000
Burned	8	1	T8	0.827	0.820
Burned	8	2	T1	0.000	0.000
Burned	8	2	T2	1.000	1.000
Burned	8	2	T3	1.000	0.571
Burned	8	2	T4	0.000	0.000
Burned	8	2	T5	0.071	0.000
Burned	8	2	T6	1180.000	0.000
Burned	8	2	T8	0.820	0.818
Burned	8	3	T1	0.000	0.000
Burned	8	3	T2	0.000	0.000
Burned	8	3	T3	0.833	0.000
Burned	8	3	T4	0.000	0.000
Burned	8	3	T5	0.000	0.000
Burned	8	3	T6	1180.000	0.000
Burned	8	3	T8	0.934	0.681
Burned	8	4	T1	0.010	0.000
Burned	8	4	T2	1.000	1.000
Burned	8	4	T3	1.000	1.000
Burned	8	4	T4	1.000	0.000
Burned	8	4	T5	0.111	0.056
Burned	8	4	T6	336.000	924.000
Burned	8	4	T8	0.629	0.777
Burned	8	5	T1	0.000	0.000
Burned	8	5	T2	1.000	1.000
Burned	8	5	T3	0.842	0.341
Burned	8	5	T4	0.000	0.000
Burned	8	5	T5	0.012	0.000
Burned	8	5	T6	1180.000	0.000
Burned	8	5	T8	0.795	0.430

Burned	8	6	T1	0.000	0.000
Burned	8	6	T2	1.000	1.000
Burned	8	6	T3	1.000	0.642
Burned	8	6	T4	0.000	0.000
Burned	8	6	T5	0.038	0.057
Burned	8	6	T6	2863.000	0.000
Burned	8	6	T8	0.966	0.751
Burned	8	7	T1	0.000	0.000
Burned	8	7	T2	1.000	1.000
Burned	8	7	T3	1.000	1.000
Burned	8	7	T4	0.000	0.000
Burned	8	7	T5	0.053	0.000
Burned	8	7	T6	1180.000	0.000
Burned	8	7	T8	0.698	0.571
Burned	8	8	T1	0.000	0.000
Burned	8	8	T2	1.000	1.000
Burned	8	8	T3	1.000	0.607
Burned	8	8	T4	0.000	0.000
Burned	8	8	T5	0.018	0.000
Burned	8	8	T6	1180.000	0.000
Burned	8	8	T8	0.820	0.919
Burned	8	9	T1	0.000	0.000
Burned	8	9	T2	0.000	0.000
Burned	8	9	T3	0.875	0.625
Burned	8	9	T4	0.000	0.000
Burned	8	9	T5	0.250	0.000
Burned	8	9	T6	1180.000	0.000
Burned	8	9	T8	0.411	0.592
Burned	8	10	T1	0.000	0.000
Burned	8	10	T2	1.000	1.000
Burned	8	10	T3	1.000	0.478
Burned	8	10	T4	0.000	0.000
Burned	8	10	T5	0.044	0.043
Burned	8	10	T6	1180.000	0.000
Burned	8	10	T8	0.240	0.590
Burned	10	1	T1	0.000	0.000
Burned	10	1	T2	0.000	0.000
Burned	10	1	T3	0.000	0.000
Burned	10	1	T4	0.000	0.000
Burned	10	1	T5	1.000	0.000
Burned	10	1	T6	1823.000	0.000
Burned	10	1	T8	0.820	0.544
Burned	10	2	T1	0.000	0.000
Burned	10	2	T2	0.000	0.000
Burned	10	2	T3	1.000	0.000
Burned	10	2	T4	0.000	0.000
Burned	10	2	T5	0.000	0.000
Burned	10	2	T6	1823.000	0.000
Burned	10	2	T8	0.820	0.820

Burned	10	3	T1	0.000	0.000
Burned	10	3	T2	1.000	0.000
Burned	10	3	T3	1.000	0.000
Burned	10	3	T4	0.000	0.000
Burned	10	3	T5	0.000	0.000
Burned	10	3	T6	1823.000	0.000
Burned	10	3	T8	0.089	0.821
Burned	10	4	T1	0.000	0.000
Burned	10	4	T2	0.000	0.000
Burned	10	4	T3	0.750	0.250
Burned	10	4	T4	0.000	0.000
Burned	10	4	T5	0.500	0.000
Burned	10	4	T6	1823.000	0.000
Burned	10	4	T8	0.698	0.820
Burned	10	5	T1	0.000	0.000
Burned	10	5	T2	0.000	0.000
Burned	10	5	T3	1.000	0.000
Burned	10	5	T4	0.000	0.000
Burned	10	5	T5	0.000	0.000
Burned	10	5	T6	1823.000	0.000
Burned	10	5	T8	0.820	0.693
Burned	10	6	T1	0.000	0.000
Burned	10	6	T2	0.000	0.000
Burned	10	6	T3	1.000	0.750
Burned	10	6	T4	1.000	0.000
Burned	10	6	T5	0.000	0.000
Burned	10	6	T6	1823.000	0.000
Burned	10	6	T8	0.649	0.969
Burned	10	7	T1	0.000	0.000
Burned	10	7	T2	0.000	0.000
Burned	10	7	T3	0.952	0.408
Burned	10	7	T4	0.400	0.000
Burned	10	7	T5	0.039	0.049
Burned	10	7	T6	1823.000	0.000
Burned	10	7	T8	0.763	0.885
Burned	10	8	T1	0.000	0.000
Burned	10	8	T2	0.000	0.000
Burned	10	8	T3	0.333	1.000
Burned	10	8	T4	0.000	0.000
Burned	10	8	T5	1.000	0.000
Burned	10	8	T6	1823.000	0.000
Burned	10	8	T8	0.592	0.624
Burned	10	9	T1	0.000	0.000
Burned	10	9	T2	0.000	0.000
Burned	10	9	T3	0.000	0.000
Burned	10	9	T4	1.000	0.000
Burned	10	9	T5	0.000	0.000
Burned	10	9	T6	1823.000	0.000
Burned	10	9	T8	0.736	0.912

Burned	10	10	T1	0.000			0.000
Burned	10	10	T2	0.000			0.000
Burned	10	10	T3	0.200			0.000
Burned	10	10	T4	0.000			0.000
Burned	10	10	T5	0.100			0.000
Burned	10	10	T6	1823.000			0.000
Burned	10	10	T8	0.251			0.532
Meadow	5	1	T1	0.000	0.000	0.000	0.000
Meadow	5	1	T2	0.000	0.000	0.000	0.000
Meadow	5	1	T3	0.500	1.000	0.000	0.000
Meadow	5	1	T4	0.000	0.000	0.000	0.000
Meadow	5	1	T5	0.000	0.000	0.000	0.000
Meadow	5	1	T6	3381.000	0.000	0.000	0.000
Meadow	5	1	T8	0.880	0.880	0.880	0.880
Meadow	5	2	T1	0.000	0.000	0.000	0.000
Meadow	5	2	T2	0.000	0.000	1.000	0.000
Meadow	5	2	T3	1.000	0.250	1.000	1.000
Meadow	5	2	T4	1.000	0.000	0.000	0.000
Meadow	5	2	T5	0.000	0.000	0.000	0.000
Meadow	5	2	T6	3381.000	0.000	0.000	0.000
Meadow	5	2	T8	0.880	0.880	0.880	0.880
Meadow	5	3	T1	0.000	0.000	0.000	0.000
Meadow	5	3	T2	0.000	0.000	1.000	1.000
Meadow	5	3	T3	1.000	0.500	0.750	1.000
Meadow	5	3	T4	1.000	0.000	0.000	0.000
Meadow	5	3	T5	0.000	0.000	0.000	0.000
Meadow	5	3	T6	3381.000	0.000	0.000	0.000
Meadow	5	3	T8	0.880	0.880	0.880	0.880
Meadow	5	4	T1	0.000	0.000	0.000	0.000
Meadow	5	4	T2	0.000	1.000	0.000	0.000
Meadow	5	4	T3	1.000	0.667	0.500	0.000
Meadow	5	4	T4	1.000	0.000	0.000	0.000
Meadow	5	4	T5	0.000	0.000	0.000	0.000
Meadow	5	4	T6	3381.000	0.000	0.000	0.000
Meadow	5	4	T8	0.880	0.880	0.880	0.880
Meadow	5	5	T1	0.000	0.000	0.000	0.000
Meadow	5	5	T2	0.000	0.000	0.000	0.000
Meadow	5	5	T3	1.000	0.000	0.000	0.000
Meadow	5	5	T4	0.000	0.000	0.000	0.000
Meadow	5	5	T5	0.000	0.000	0.000	0.000
Meadow	5	5	T6	3381.000	0.000	0.000	0.000
Meadow	5	5	T8	0.880	0.880	0.880	0.880

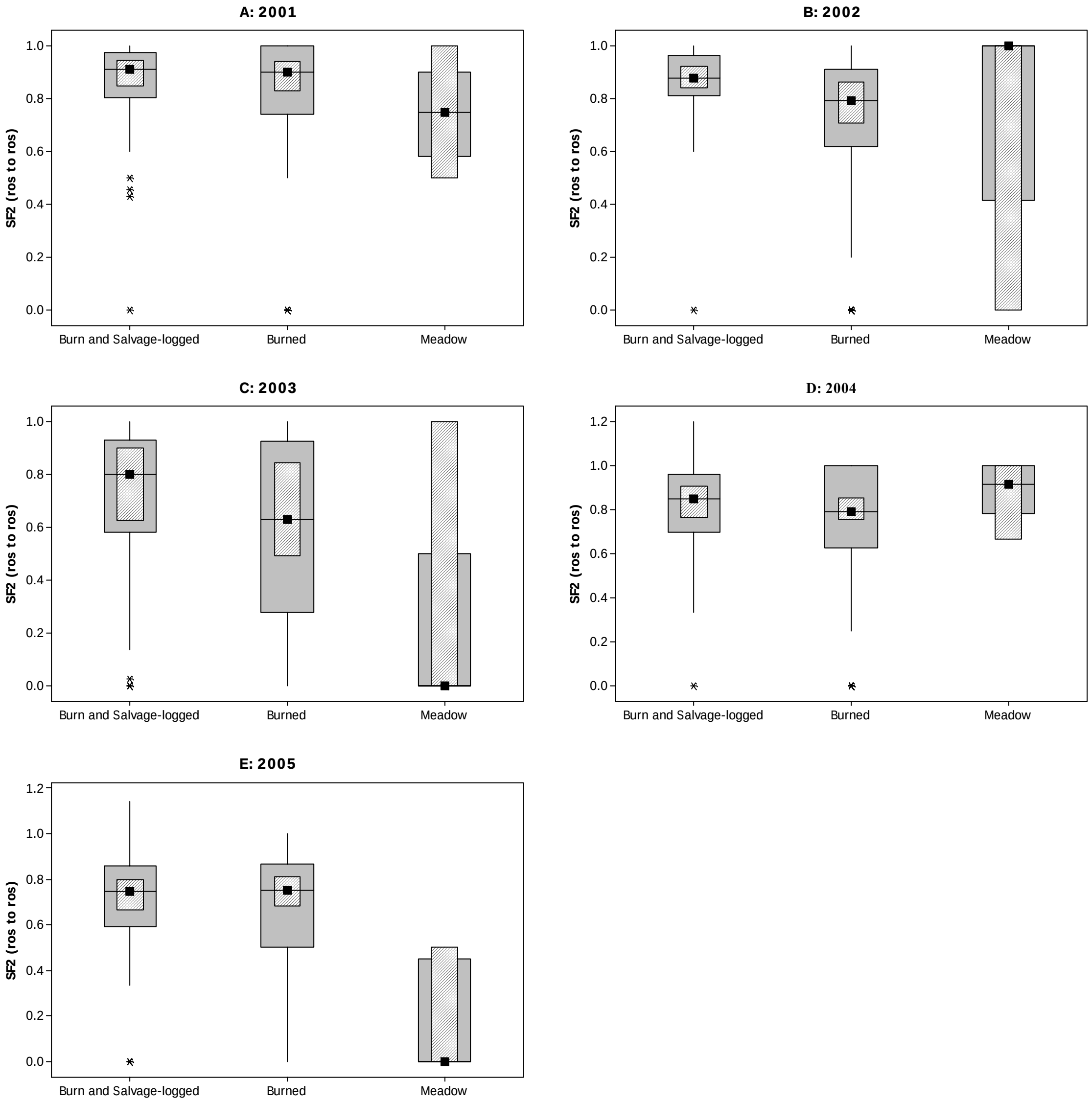


Figure D.1. Transition rates from spring-to-fall rosette to rosette transition rate (SF2) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

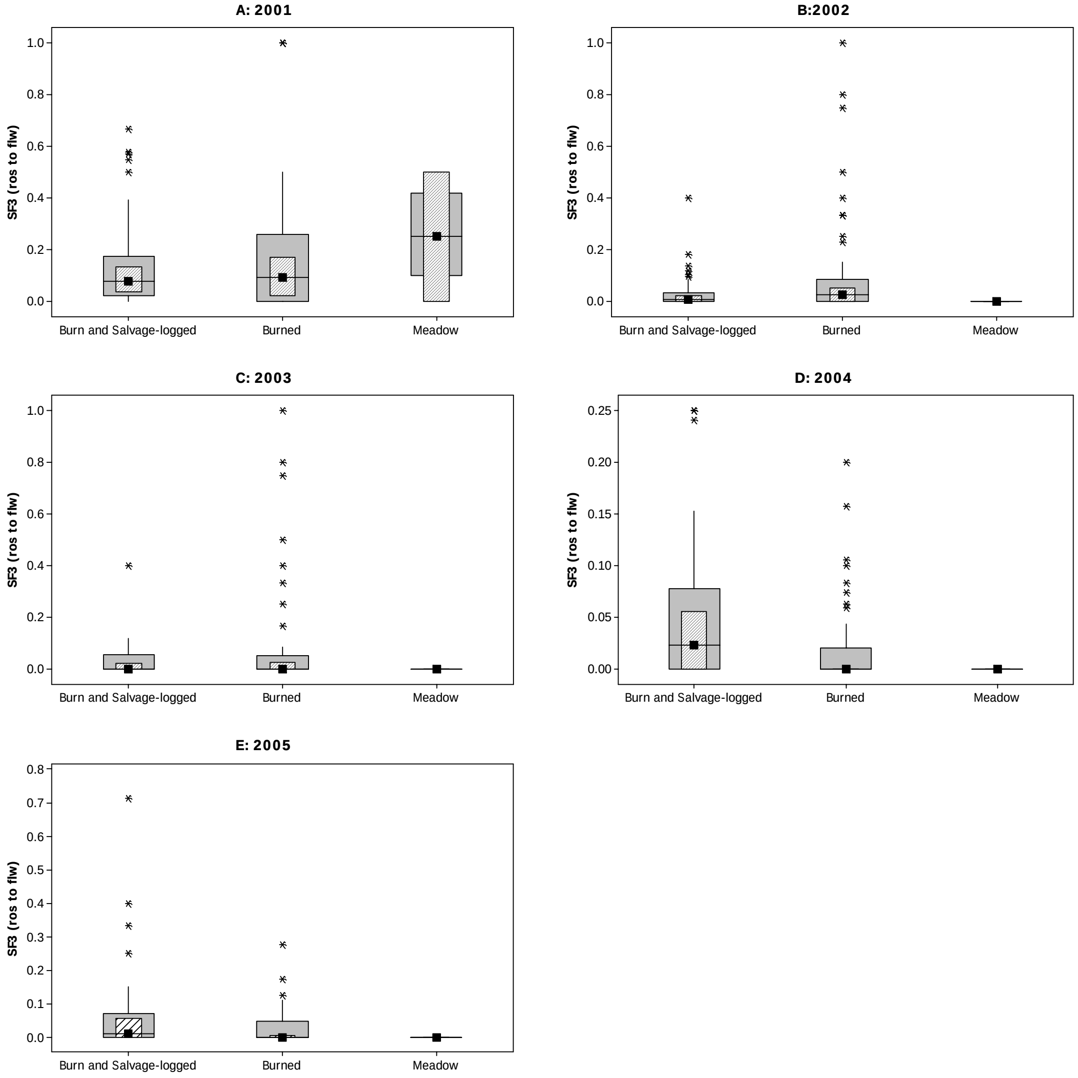


Figure D.2. Transition rates from spring-to-fall rosette to flowering transition rate (SF3) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

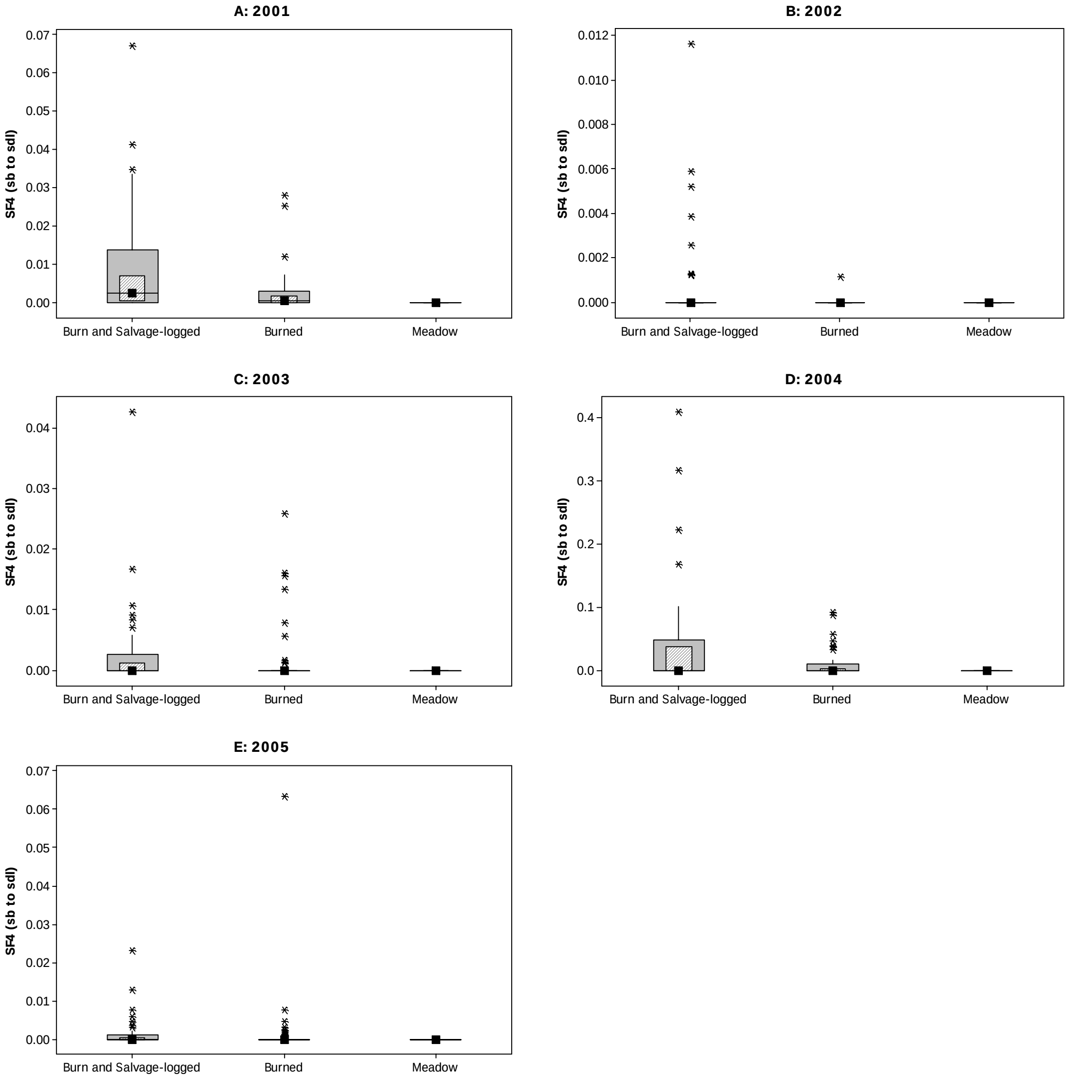


Figure D.3. Transition rates from spring-to-fall seed bank to seedling transition rate (SF4) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

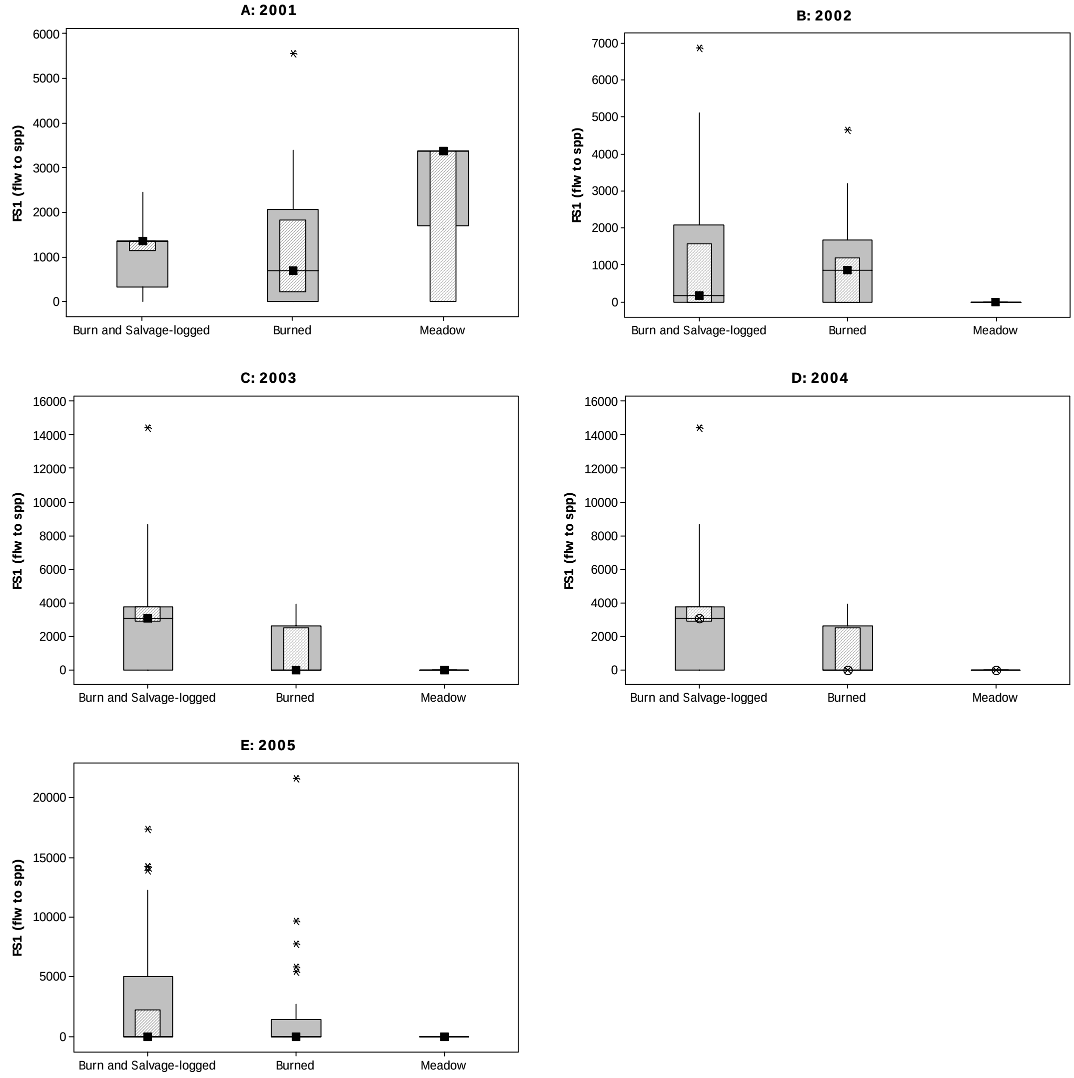


Figure D.4. Transition rates from fall-to-spring flowering to seed produced rate (FS1) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

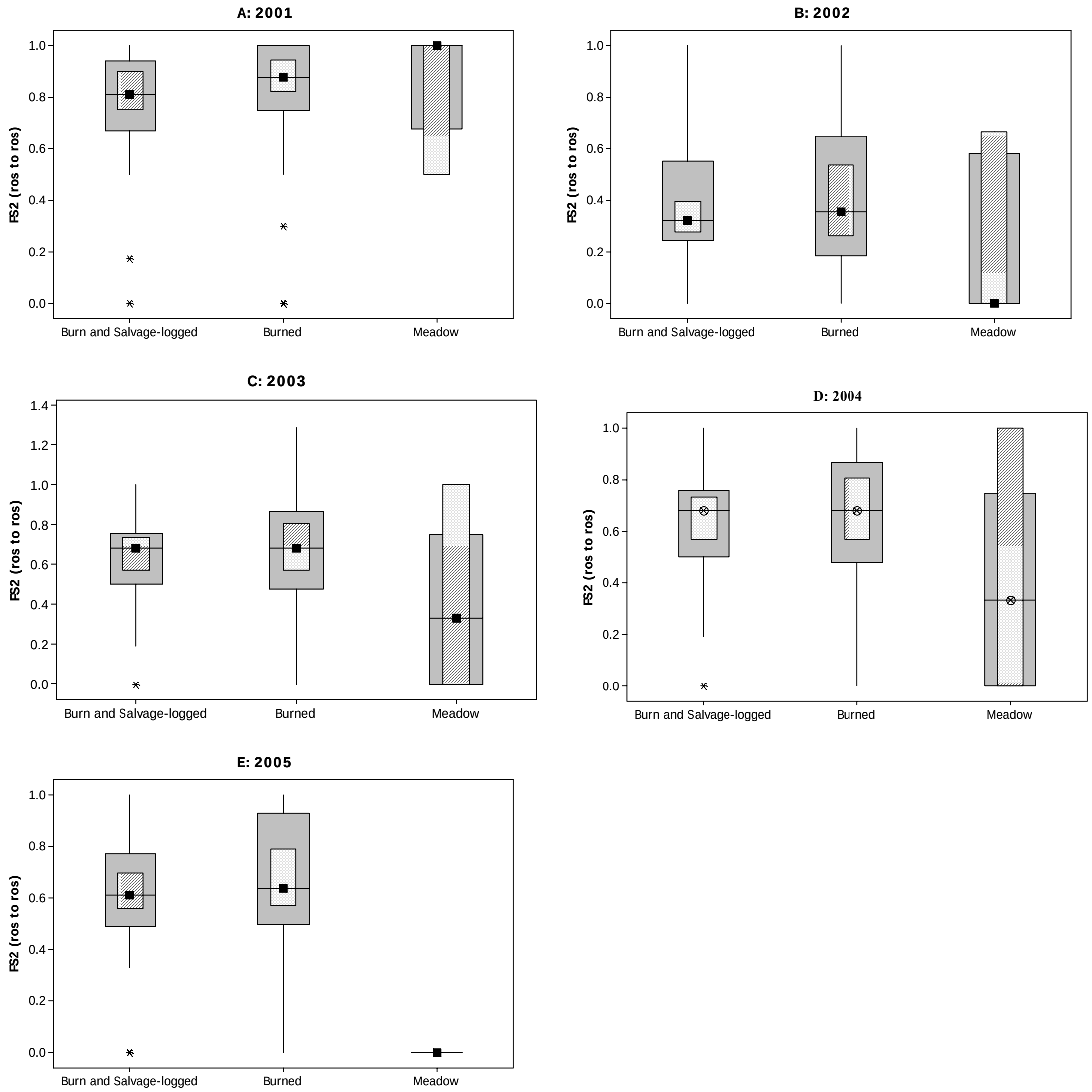


Figure D.5. Transition rates from fall-to-spring rosette to rosette transition rate (FS2) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

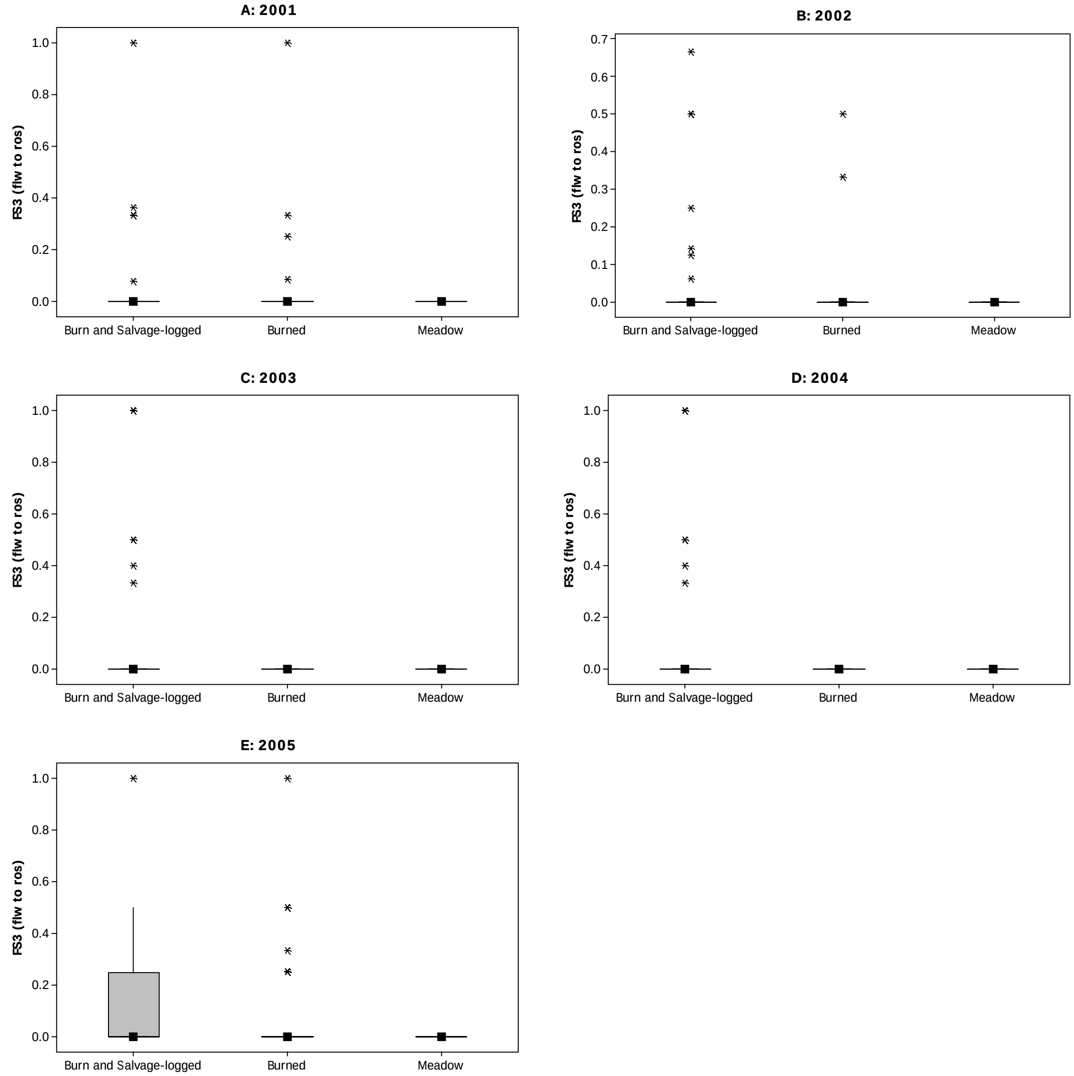


Figure D.6. Transition rates from fall-to-spring flowering to rosette transition rate (FS3) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

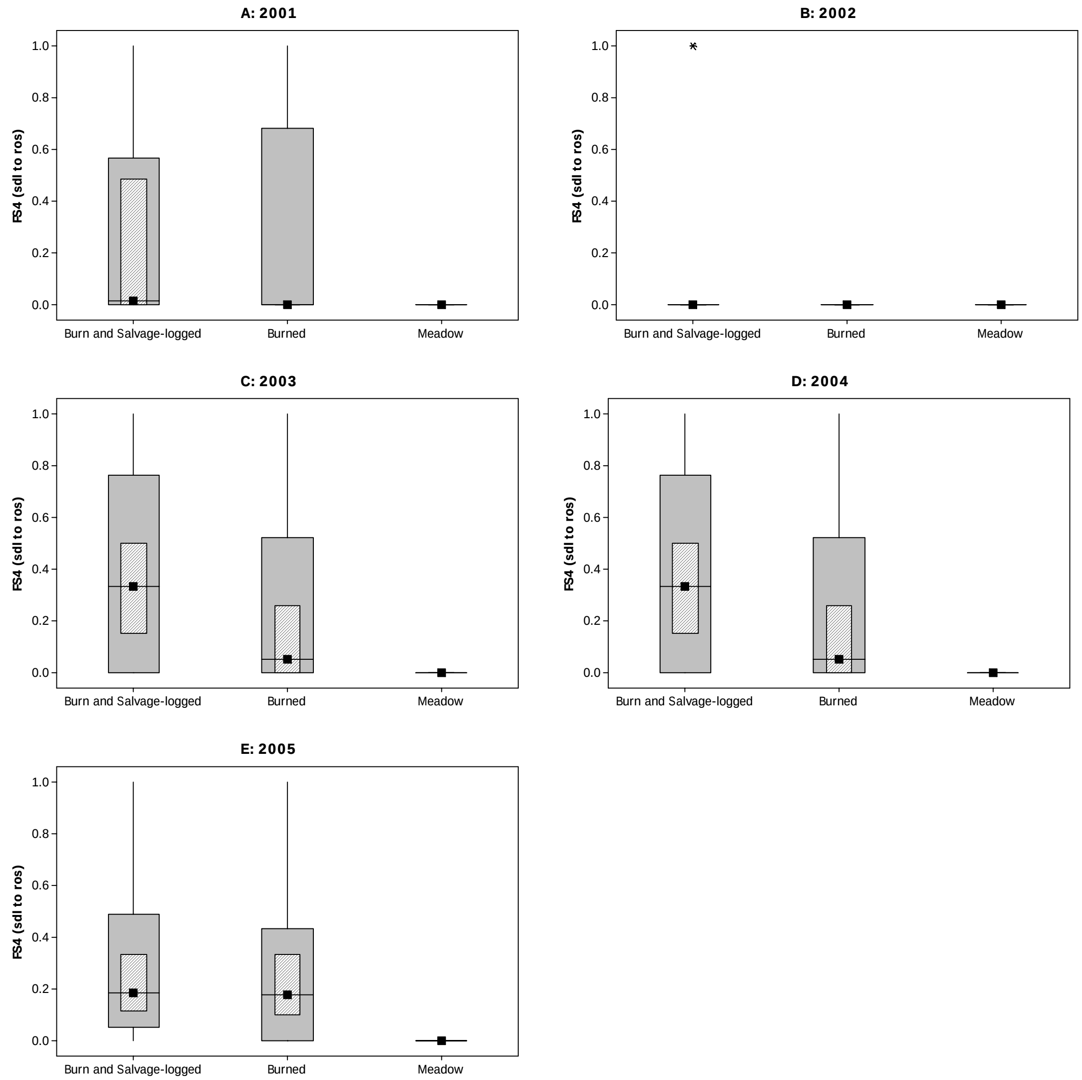


Figure D.7. Transition rates from fall-to-spring seedling to rosette transition rate (FS4) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

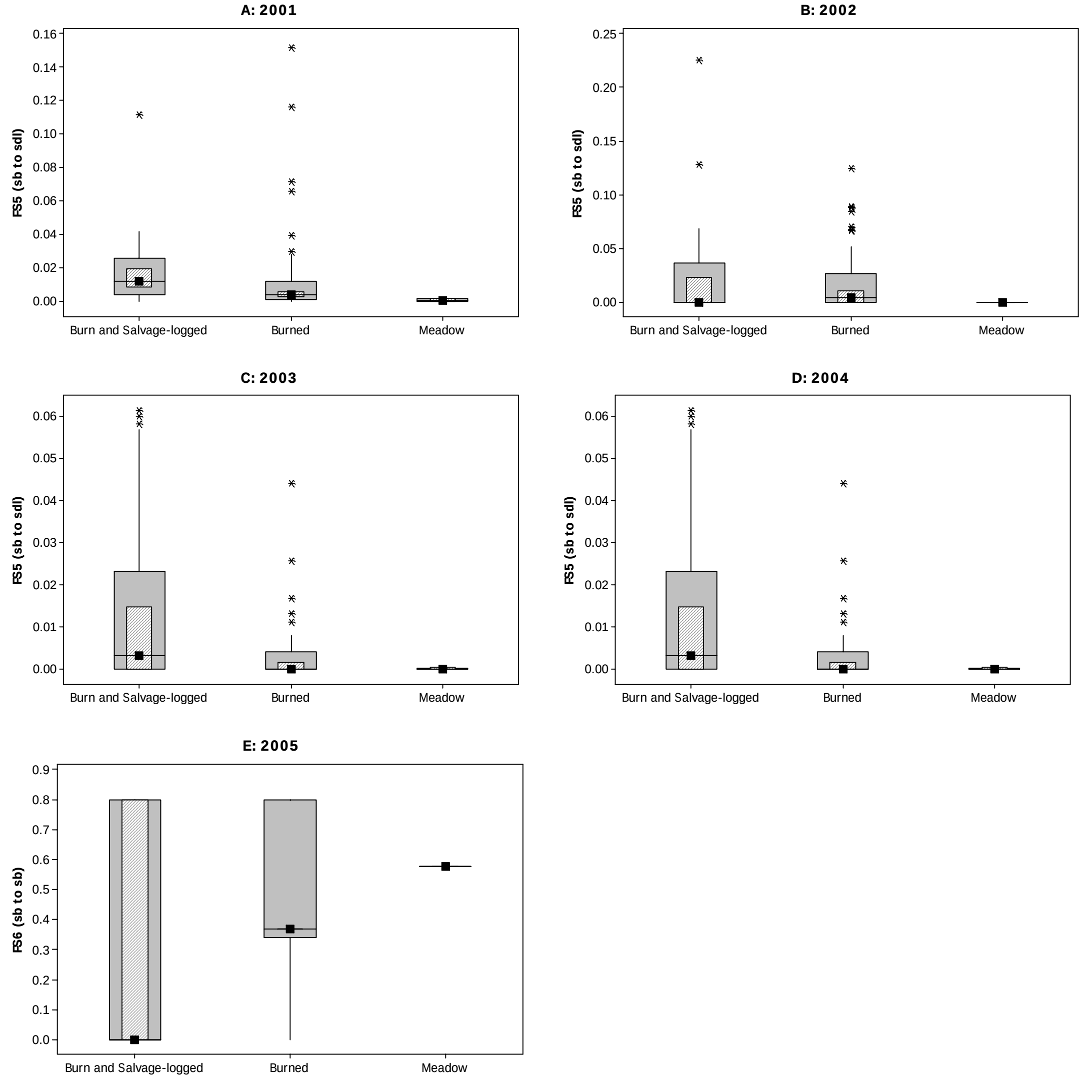


Figure D.8. Transition rates from fall-to-spring seed bank to seedling transition rate (FS5) for 2001, n = 95 (A), 2002, n = 95 (B), 2003, n = 45 (C), 2004, n = 94 (D), and 2005, n = 94 (E). Shown are the median (central line and box), 50 % of the data (light shaded box), data within the first and third quartile (vertical lines), outlier (stars), and 95 % confidence interval for the median (hatched box) across environments. If the confidence intervals do not overlap, the two responses were judged to be significantly different.

APPENDIX E

MONTHLY CLIMATE DATA

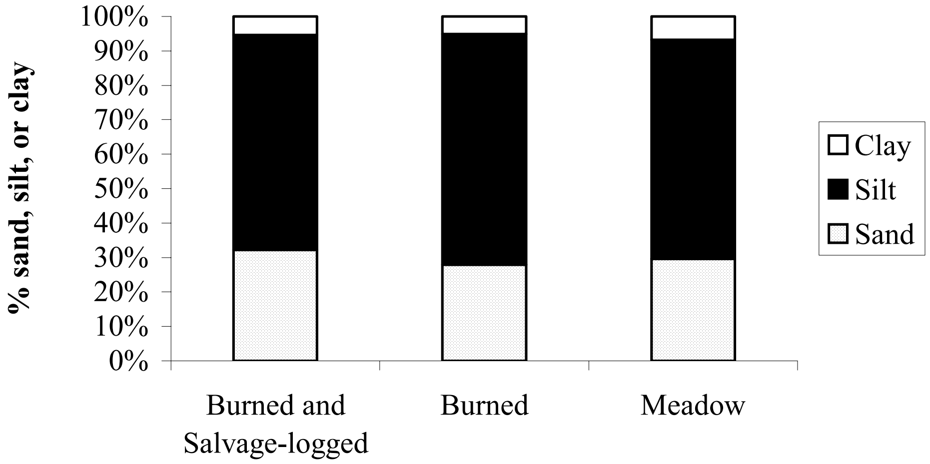
Table E.1. Mean (± standard deviation) monthly precipitation (cm) and mean (± standard deviation), mean minimum (± standard deviation), and mean maximum (± standard deviation) temperature (^{o}C) for 2000 through 2005 from the Libby 32 SSE, Montana weather station near the study area.

	January	February	March	April	May	June	July	August	September	October	November	December
Mean Precipitation	5.7 (2.17)	3.0 (2.02)	5.1 (3.00)	3.9 (0.99)	5.7 (3.70)	4.1 (2.02)	1.5 (1.29)	1.6 (1.93)	2.4 (1.02)	3.7 (2.84)	3.9 (2.74)	5.6 (1.07)
Mean Temperature	-5.5 (1.18)	-3.7 (1.49)	0.5 (1.81)	4.9 (0.94)	8.9 (0.70)	12.4 (0.80)	15.3 (1.06)	14.8 (1.70)	10.3 (1.02)	4.6 (1.95)	-1.8 (2.83)	-5.7 (2.77)
Minimum Temperature	-9.4 (1.44)	-11.3 (1.57)	-5.4 (1.66)	-2.5 (0.41)	0.5 (0.76)	3.0 (0.98)	4.8 (1.59)	3.3 (2.01)	0.4 (0.71)	-3.8 (2.86)	-7.2 (2.75)	-8.8 (3.87)
Maximum Temperature	0.0 (1.05)	2.9 (1.87)	7.0 (2.25)	13.0 (2.00)	17.2 (1.60)	21.4 (1.18)	27.0 (1.49)	26.3 (3.21)	20.5 (2.37)	12.4 (1.63)	3.2 (2.94)	-0.6 (1.82)

APPENDIX F

SOIL CHARATERISTICS ANALYSIS

A: Soil texture



B: CEC species

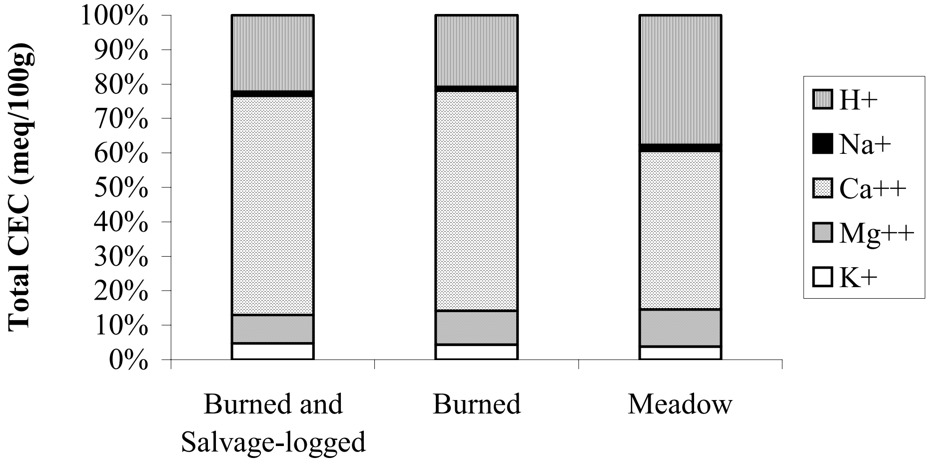


Figure F.1. Mean percent sand, silt, and clay (A) and mean CEC species (B) by environment.

All Environments (A)

	SF2	FS2	N_ppm	Olsen_P_ppm	K_ppm
SF2	1	-0.032923794	0.23311791	0.036695258	-0.0591544
FS2	-0.03292379	1	0.00706058	0.003342525	-0.08265845
N_ppm	0.23311791	0.007060581	1	0.033911715	0.29160942
Olsen_P_ppm	0.03669526	0.003342525	0.03391172	1	0.3222225
K_ppm	-0.0591544	-0.082658451	0.29160942	0.322222499	1

Burned and Salvage-logged (B)

	SF2	FS2	N_ppm	Olsen_P_ppm	K_ppm
SF2	1	0.11861097	0.07206901	-0.01186444	-0.0768232
FS2	0.11861097	1	0.12806272	-0.02563743	-0.1154625
N_ppm	0.07206901	0.12806272	1	-0.15562429	0.1796223
Olsen_P_ppm	-0.01186444	-0.02563743	-0.15562429	1	0.2139351
K_ppm	-0.07682319	-0.11546246	0.17962234	0.21393514	1

Burned (C)

	SF2	FS2	N_ppm	Olsen_P_ppm	K_ppm
SF2	1	-0.11733319	0.1894899	-0.12262328	-0.25992127
FS2	-0.1173332	1	-0.1320878	0.06613777	-0.05281764
N_ppm	0.1894899	-0.13208777	1	-0.2038741	0.27571631
Olsen_P_ppm	-0.1226233	0.06613777	-0.2038741	1	0.3249102
K_ppm	-0.2599213	-0.05281764	0.2757163	0.3249102	1

Meadow (D)

	SF2	FS2	N_ppm	Olsen_P_ppm	K_ppm
SF2	1	-0.11733319	0.1894899	-0.12262328	-0.25992127
FS2	-0.1173332	1	-0.1320878	0.06613777	-0.05281764
N_ppm	0.1894899	-0.13208777	1	-0.2038741	0.27571631
Olsen_P_ppm	-0.1226233	0.06613777	-0.2038741	1	0.3249102
K_ppm	-0.2599213	-0.05281764	0.2757163	0.3249102	1

Figure F.2. Pearson correlation matrix for selected soil charaterstics and rosette to rosette survival (FS2 and SF2) for all envrionemts (A), the Burned and Salvage-logged (B), the Burned (C), and the Meadow (D) enviroments for 2002.

All Environments (A)

	Precip	PrePrecip	Year	SF2	FS2
Precip	1	0.474289	0.490617	-0.086564	-0.048107
PrePrecip	0.474289	1	0.978437	-0.161968	-0.186048
Year	0.490617	0.978437	1	-0.182062	-0.121412
SF2	-0.086564	-0.161968	-0.182062	1	0.248779
FS2	-0.048107	-0.186048	-0.121412	0.248779	1

Burned and Salvage-logged (B)

	Precip	PrePrecip	Year	SF2	FS2
Precip	1	0.474289	0.490617	-0.097036	-0.01515
PrePrecip	0.474289	1	0.978437	-0.183189	-0.16541
Year	0.490617	0.978437	1	-0.21659	-0.087786
SF2	-0.097036	-0.183189	-0.21659	1	0.113545
FS2	-0.01515	-0.16541	-0.087786	0.113545	1

Burned (C)

	Precip	PrePrecip	Year	SF2	FS2
Precip	1	0.474289	0.490617	-0.103181	-0.028576
PrePrecip	0.474289	1	0.978437	-0.144064	-0.140647
Year	0.490617	0.978437	1	-0.148626	-0.080629
SF2	-0.103181	-0.144064	-0.148626	1	0.309263
FS2	-0.028576	-0.140647	-0.080629	0.309263	1

Meadow (D)

	Precip	PrePrecip	Year	SF2	FS2
Precip	1	0.474289	0.490617	0.051559	-0.119258
PrePrecip	0.474289	1	0.978437	-0.258513	-0.618649
Year	0.490617	0.978437	1	-0.339011	-0.56744
SF2	0.051559	-0.258513	-0.339011	1	0.144939
FS2	-0.119258	-0.618649	-0.56744	0.144939	1

Figure F.3. Pearson correlation matrix for selected time and rosette to rosette survival (SF2 and FS2) for all envrionemts (A), the Burned and Salvage-logged (B), the Burned (C), and the Meadow enviroments (D) 2001 through 2005.

All Environments (A)

	FS2	SF2	Percent_OM	pH	CEC
FS2	1	0.26383959	0.0707311	-0.06788552	-0.008360868
SF2	0.263839593	1	-0.02882714	-0.06166023	-0.106933347
Percent_OM	0.070731102	-0.02882714	1	-0.27845106	0.672135794
pH	-0.06788552	-0.06166023	-0.27845106	1	-0.026081361
CEC	-0.008360868	-0.10693335	0.67213579	-0.02608136	1

Burned and Salvage-logged (B)

	FS2	SF2	Percent_OM	pH	CEC
FS2	1	0.10158904	0.12455632	-0.0242288	0.05448963
SF2	0.10158904	1	0.02170987	-0.12740857	0.03321385
Percent_OM	0.12455632	0.02170987	1	-0.05752757	0.70105366
pH	-0.0242288	-0.12740857	-0.05752757	1	0.09798335
CEC	0.05448963	0.03321385	0.70105366	0.09798335	1

Burned (C)

	FS2	SF2	Percent_OM	pH	CEC
FS2	1	0.335073466	0.088995202	-0.20937031	-0.04936365
SF2	0.33507347	1	0.005225745	-0.13770819	-0.20802029
Percent_OM	0.0889952	0.005225745	1	-0.35395271	0.65955665
pH	-0.20937031	-0.137708188	-0.353952707	1	-0.08662953
CEC	-0.04936365	-0.208020295	0.659556653	-0.08662953	1

Meadow (D)

	FS2	SF2	Percent_OM	pH	CEC
FS2	1	0.3185517	0.1916851	0.09438258	0.1855636
SF2	0.31855166	1	-0.1158049	0.3029107	-0.1110775
Percent_OM	0.1916851	-0.1158049	1	-0.40143758	0.9964956
pH	0.09438258	0.3029107	-0.4014376	1	-0.4391876
CEC	0.18556364	-0.1110775	0.9964956	-0.43918758	1

Figure F.4. Pearson correlation matrix for selected time and rosette to rosette survival (SF2 and FS2) for all envrionemts (A), the Burned and Salvage-logged (B), the Burned (C), and the Meadow enviroments (D) 2001 through 2005.

APPENDIX G

LOCATION OF ENVIRONMENT PLOTS

Plot ID	Site Type	Attribute	Latitude	Longitude
1d012	Burned		48.31644657	-114.8693845
2d012	Burned		48.31651168	-114.8694688
3d012	Burned	Sprayed w BT 2004 & 2005	48.31649297	-114.8695394
4d012	Burned	Sprayed w BT 2004 & 2005	48.31645328	-114.8695444
5d012	Burned	Sprayed w BT 2004 & 2005	48.31637469	-114.8695629
6d012	Burned	Sprayed w BT 2004 & 2005	48.31626421	-114.8696733
7d012	Burned		48.31627395	-114.8697233
8d012	Burned		48.3162593	-114.8697174
9d012	Burned	Sprayed w BT 2004 & 2005	48.3162437	-114.8696872
10d012	Burned		48.31623804	-114.8698127
1d011	Burned & Salvaged		48.30815154	-114.8643697
2d011	Burned & Salvaged	Sprayed w BT 2004 & 2005	48.30811451	-114.8643987
3d011	Burned & Salvaged		48.30810241	-114.8644406
4d011	Burned & Salvaged		48.30808584	-114.8644889
5d011	Burned & Salvaged	Sprayed w BT 2004 & 2005	48.30807646	-114.8644587
6d011	Burned & Salvaged	Sprayed w BT 2004 & 2005	48.30805741	-114.8644708
7d011	Burned & Salvaged	Sprayed w BT 2004 & 2005	48.30806709	-114.8644325
8d011	Burned & Salvaged		48.30808155	-114.8643855
9d011	Burned & Salvaged		48.30806592	-114.8643385
10d011	Burned & Salvaged	Sprayed w BT 2004 & 2005	48.30810112	-114.8643217
1c014	Burned	Sprayed w BT 2005	48.30690774	-114.8718665
2c014	Burned	Sprayed w BT 2005	48.30687148	-114.8718278
3c014	Burned	Sprayed w BT 2005	48.30691304	-114.8717958
4c014	Burned		48.30692065	-114.8717126
5c014	Burned		48.30689732	-114.8717122
6c014	Burned	Sprayed w BT 2005	48.3069383	-114.8716863
7c014	Burned		48.30692149	-114.8716851
8c014	Burned		48.30696267	-114.8717243
9c014	Burned	Sprayed w BT 2005	48.30695054	-114.871774
10c014	Burned		48.30695617	-114.8719442
1c011	Burned & Salvaged		48.30422313	-114.8699287
2c011	Burned & Salvaged		48.3042428	-114.8698538
3c011	Burned & Salvaged		48.30423118	-114.869759
4c011	Burned & Salvaged		48.30423321	-114.8697006
5c011	Burned & Salvaged		48.30426078	-114.8696022
6c011	Burned & Salvaged		48.3043492	-114.8696679
7c011	Burned & Salvaged		48.30441162	-114.8697371
8c011	Burned & Salvaged		48.30436046	-114.869918
9c011	Burned & Salvaged		48.30443023	-114.8700475
1c012	Burned		48.30420921	-114.8707506
2c012	Burned		48.30416483	-114.8707887
3c012	Burned		48.30424354	-114.8708835
4c012	Burned		48.30425009	-114.870935
5c012	Burned		48.30417914	-114.8709288
6c012	Burned		48.30413111	-114.8708538
8c012	Burned		48.30427118	-114.8709642
7c012	Burned		48.30416097	-114.8709918
9c012	Burned		48.30420297	-114.871007

10c012	Burned	48.30422046	-114.8710446
1a011	Burned & Salvaged	48.28681319	-114.8767701
2a011	Burned & Salvaged	48.28685685	-114.8768854
3a011	Burned & Salvaged	48.28679938	-114.8769287
4a011	Burned & Salvaged	48.2868157	-114.8769534
5a011	Burned & Salvaged	48.28686262	-114.8770679
6a011	Burned & Salvaged	48.28682543	-114.8770938
7a011	Burned & Salvaged	48.28678413	-114.8770841
8a011	Burned & Salvaged	48.28672806	-114.8771377
9a011	Burned & Salvaged	48.28674708	-114.87719
10a011	Burned & Salvaged	48.28672739	-114.8772621
1a012	Burned	48.28130046	-114.868641
2a012	Burned	48.28127756	-114.8686621
3a012	Burned	48.28118178	-114.8688601
4a012	Burned	48.28113456	-114.8690507
5a012	Burned	48.28108352	-114.8690522
6a012	Burned	48.28113056	-114.8691113
7a012	Burned	48.28102178	-114.8691963
8a012	Burned	48.28098642	-114.86932
9a012	Burned	48.2809825	-114.8693749
10a012	Burned	48.28100033	-114.8694493
1a011b	Burned & Salvaged	48.28049382	-114.866346
2a011b	Burned & Salvaged	48.28054784	-114.8663906
3a011b	Burned & Salvaged	48.28052938	-114.8662991
4a011b	Burned & Salvaged	48.28053973	-114.8662663
5a011b	Burned & Salvaged	48.28046327	-114.8662359
6a011b	Burned & Salvaged	48.28041955	-114.8662039
7a011b	Burned & Salvaged	48.28038594	-114.8661763
8a011b	Burned & Salvaged	48.280334	-114.8661409
9a011b	Burned & Salvaged	48.28035511	-114.8662865
10a011b	Burned & Salvaged	48.28043268	-114.866284
1a011a	Burned	48.27995947	-114.8669618
2a011a	Burned	48.28000471	-114.8669351
3a011a	Burned	48.28005163	-114.8669136
4a011a	Burned	48.28009164	-114.8669742
5a011a	Burned	48.28011973	-114.8670195
6a011a	Burned	48.28020314	-114.8668709
7a011a	Burned	48.28012779	-114.8668227
8a011a	Burned	48.2801274	-114.8667574
9a011a	Burned	48.27999819	-114.8667216
10a011a	Burned	48.27993404	-114.8666812
1a0115	Meadow	48.27978619	-114.8673774
2a0115	Meadow	48.27979988	-114.8673054
3a0115	Meadow	48.27973395	-114.8671526
4a0115	Meadow	48.27974871	-114.8670939
5a0115	Meadow	48.27982415	-114.8671163

APPENDIX H

LOCATION OF DATA

Data found in \\seedbank\D\Experiments\Libby\Bauer

- \Chapter_1
  - Endnote File
- \Chapter_2
  - AIC calculations
  - Analysis of variables used in habitat model
- \Chapter_3_&_6
  - \Capitulum
    - Capitulum and seed counts from 2004 & 2005
  - \Climate
    - Climate data from Libby weather station
  - \Growth_Rate_Site_Location
    - GPS location of plots and writing directions
  - \Matrix_Model
    - Box plots of fall to fall transitions
    - \Model_in_R
      - R model and data for matrix model using fall to fall transitions
    - \Transition_Calculation
      - Worksheets for calculating fall to fall transitions
  - \Seedbank
    - Buried seed germination rate for 2004 & 2005
  - \Summer04
    - Worksheets for calculating 2004 transitions
  - \Summer05+Difference_Model
    - Difference Equation
    - All transitions used from 2001 to 2005
    - \Transition_Calculation
      - Worksheets for calculating 2005 transitions
- \Chapter_4
  - \Density_Dependence
    - Intra and Inter-specific density dependence
  - \Percent_Cover
    - Percent cover from 2004 & 2005
  - \PercentSky
    - Percent sky from 2004 & 2005
  - \Precip
    - Correlations of precipitations and transition rates
  - \Soil
    - Results of soil test
    - Correlations of soil characteristics and transition rates
- \Chapter_5
  - Results of simulated population growth rate with increased seeding rate
  - \Slashpile04
    - Data and analysis for 2004 slash pile

- \Slashpile05
    - Data and analysis for 2005 slash pile
- \SlashpileSeedGermination
    - Germination trials for seed used in slash piles

\Chapter_6
- Location of BT spraying
- Location of biological control release sites

\Invasivness_Index_04
- Calculation of invasiveness index using transitions through 2004

\Logistic_Growth
- Logistic growth equation applied to transitions through 2004

\Reports
- Forest Service report from 2004 & 2005

\Species_Area_Curve
- Investigation into species area curve and number of NIS

ArcView GIS data found on\\tansy\c\Lincoln

Project 1: Projection: Stateplane
- View 1: 2004 & 2005 Survey Transects (Chapter 2)
    - Environment Transects (Chapter 3)
    - USFS Roads
    - Study Area Extent (Chapter 2)
    - Estimated Wildfire Extent (Chapter 2)
    - 2004 Slashpile (Chapter 5)
    - MrSid Files
- View 2: Study Area Extent (Chapter 2)
    - State Map
- Layout 2: Little Wolf Tansy Ragwort Study Area Poster (Chapter 2 & 3)

Kootenai2004: Projection: UTM
- View 1: State Map
- View 2: Tansy Ragwort Probability Map (Chapter 2)
    - 2004 & 2005 Transects (Chapter 2)
    - Roads
    - Habitat Layer
    - Remote Sensing Layers (Chapter 2)
    - DEM Layers (Chapter 2)
    - Environment Transects (Chapter 3)
- Layout 2: Tansy Ragwort Rose Diagram (Chapter 2)
- Layout 3: Tansy Ragwort Probability Map (Chapter 2)