



Quantifying tansy ragwort (*Senecio jacobaea*) population dynamics and recruitment in northwestern Montana
by Meghan Ann Trainor

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Resources and Environmental Sciences
Montana State University
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Abstract:

The weed tansy ragwort (*Senecio jacobaea*) attained noxious weed status after colonizing areas burned in northwestern Montana after a 1994 wildfire. Therefore, it was important to develop a preliminary understanding of the biotic and abiotic factors that influence tansy ragwort colonization and population dynamics in burned and unburned areas. A field experiment was designed to parameterize a transition matrix model to evaluate the effects of four different environments on dynamics of tansy ragwort in northwestern Montana including areas: 1) burned and salvage-logged, 2) burned, 3) undisturbed forest, and 4) undisturbed meadow. Based upon results from the first two years, tansy ragwort was increasing (invasive) in the burned and salvage-logged and the burned environments ($\lambda > 1.0$). In the forest, the population growth rate was nearly stable ($\lambda = 1.0$) and in the meadow the growth rate was less than one, indicating a decreasing population ($\lambda < 1.0$). Elasticity analysis determined that the over-winter survival of rosettes is the most important demographic process to tansy ragwort population growth.

A greenhouse experiment was also conducted to address the subject of tansy ragwort seedling emergence in response to environments associated with fire (litter, burned litter, bare soil, heated bare soil). Tansy ragwort emergence rates were higher in litter-covered soil, burned, or unburned environments versus bare soil or heated bare soil environments. The results may parallel previous findings that tansy ragwort emerges and establishes faster in environments with higher N levels, relative air humidity, small oscillations in soil temperature, and more light. The findings do not fully explain the observation that tansy ragwort densities are higher following wildfire or are often present where slash burns occurred.

A thermal gradient plate experiment was also conducted to determine the optimum and range of temperatures where tansy ragwort seed can germinate. Results show that Montana tansy ragwort seeds respond similarly to temperature as the seeds from western Washington and The Netherlands. The lack of difference in germination response to temperature across different geographic populations raises the question of whether genotypic variability and phenotypic plasticity are factors in the success of tansy ragwort as an introduced species.

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

The weed tansy ragwort (*Senecio jacobaea*) attained noxious weed status after colonizing areas burned in northwestern Montana after a 1994 wildfire. Therefore, it was important to develop a preliminary understanding of the biotic and abiotic factors that influence tansy ragwort colonization and population dynamics in burned and unburned areas. A field experiment was designed to parameterize a transition matrix model to evaluate the effects of four different environments on dynamics of tansy ragwort in northwestern Montana including areas: 1) burned and salvage-logged, 2) burned, 3) undisturbed forest, and 4) undisturbed meadow. Based upon results from the first two years, tansy ragwort was increasing (invasive) in the burned and salvage-logged and the burned environments ($\lambda > 1.0$). In the forest, the population growth rate was nearly stable ($\lambda = 1.0$) and in the meadow the growth rate was less than one, indicating a decreasing population ($\lambda < 1.0$). Elasticity analysis determined that the over-winter survival of rosettes is the most important demographic process to tansy ragwort population growth.

A greenhouse experiment was also conducted to address the subject of tansy ragwort seedling emergence in response to environments associated with fire (litter, burned litter, bare soil, heated bare soil). Tansy ragwort emergence rates were higher in litter-covered soil, burned, or unburned environments versus bare soil or heated bare soil environments. The results may parallel previous findings that tansy ragwort emerges and establishes faster in environments with higher N levels, relative air humidity, small oscillations in soil temperature, and more light. The findings do not fully explain the observation that tansy ragwort densities are higher following wildfire or are often present where slash burns occurred.

A thermal gradient plate experiment was also conducted to determine the optimum and range of temperatures where tansy ragwort seed can germinate. Results show that Montana tansy ragwort seeds respond similarly to temperature as the seeds from western Washington and The Netherlands. The lack of difference in germination response to temperature across different geographic populations raises the question of whether genotypic variability and phenotypic plasticity are factors in the success of tansy ragwort as an introduced species.

REVIEW OF LITERATURE

Introduction

Tansy ragwort (*Senecio jacobaea* L., Asteraceae) is an introduced, herbaceous plant that has invaded and established in areas of North America, including northwestern Montana. It colonizes disturbed habitats most frequently including pastures, clearcuts, and along roadsides. This first chapter describes the origin and distribution of tansy ragwort as well as a biological description of the species and its response to various types of management. A discussion of transition matrix models and population viability analysis concludes Chapter 1. Chapter 2 describes a field experiment I conducted in which a life history model was developed for tansy ragwort in northwestern Montana. The methodology for collecting data used as input by the model, and the technique of using a population viability analysis in invasive plant ecology is detailed. Results presented demonstrate how the population growth rate (λ) of tansy ragwort differs across environments. Results presented also demonstrate the sensitivity of population size to small changes in the elements of the model, identifying vulnerable life stages in the life cycle of tansy ragwort that may be targeted to encourage population decline under an ecologically based weed management strategy. Chapter 3 describes a greenhouse experiment designed to answer questions not answered by the field study. Measurements are reported on how tansy ragwort responded to different soil surface environments associated with fire. Finally, Chapter 4 describes a temperature gradient plate experiment

designed to determine the optimum and range of temperatures where tansy ragwort seed collected in Montana can germinate.

Senecio jacobaea

Origin and Distribution

Tansy ragwort was first recorded in North America in eastern Canada around Pictou, Nova Scotia in the 1850's, most likely disseminated in ships' discharged ballast (Harris et al. 1971). Tansy ragwort is native to Europe, Asia and Siberia and is generally found in meadows in oak and conifer woodlands, livestock pastures, and roadsides (Coombs et al. 1997b). Tansy ragwort's native range extends as far north as Norway and south into Romania, Hungary, and Bulgaria (Harper and Wood 1957). It is considered rare in both the north and south extremes of its range. Tansy ragwort has been introduced into Australia, New Zealand, South Africa, South America, and North America.

Tansy ragwort is a problem on both the east and west coast of North America, in the maritime regions and particularly in Oregon. In the east, tansy ragwort is found in Newfoundland and New England and in the west from Southern British Columbia to Northern California (Bain 1991). The weed was first recorded in western North America in 1913 from Vancouver Island (Harris et al. 1971). Tansy ragwort was first recorded in Oregon in 1922 from Portland (McEvoy and Rudd 1993). In the Pacific Northwest, tansy ragwort is found from the upper beaches along the Pacific Ocean up to the 900 m level in the Cascade Mountains. The largest infestations occur west of the Cascade Mountains, but tansy ragwort is also found east of the Cascade Mountains in areas previously

considered inhospitable to its establishment. In areas east of the Cascades, tansy ragwort is generally found at disturbed sites in mountains where precipitation exceeds 40 to 51 cm per year (Coombs et al. 1997b).

Tansy ragwort was first recorded in Idaho in 1987 (Burrill et al. 1994). In 1990, tansy ragwort was first reported in Western Montana (Markin 2001). Contaminated straw and hay have been principal carriers of tansy ragwort seeds. It is speculated by some land managers that logging equipment has transported tansy ragwort seeds, as well. Open areas, south-facing slopes and disturbed areas appear to be the most vulnerable to invasion. In the western United States, Douglas fir (*Pseudotsuga menzeizii*) habitat types are a potential tansy ragwort habitat (Coombs et al. 1997b) (Figure 1).



Figure 1. Map of northwest region of North America. Shaded areas indicate counties (U.S.) or regional districts (B.C.) in which tansy ragwort has been reported.

Morphology

Tansy ragwort is herbaceous, growing 0.3 - 2 m tall, and is usually regarded as a biennial, overwintering either as seeds or rosettes. However, it is capable of perennating from the rootstock or caudex and so may behave as a true perennial (Forbes 1977).

Tansy ragwort becomes more glabrate with age, arising from a tap root. The stems are described as strict, erect, and arising singly or in clusters from an erect caudex, branching only in the inflorescence. Leaves are alternate, becoming smaller in size upward, broadly ovate to ovate, deeply bi- or tripinnatifid, 7 - 20 cm long, 2 - 6 cm wide. The lower leaves are often petiolate and early deciduous, with middle and upper leaves sessile and weakly clasping.

The inflorescence is broadly corymbiform and cymose with 20 - 60 heads. Heads are usually radiate, discs 7 - 10 mm wide, with 13, 3 - 4 mm long dark-tipped involucre bracts. The female ray florets number 13. Disc florets are numerous and perfect. The achenes of the ray florets are glabrous, while those of disc florets are pubescent along prominent ribs (Bain 1991).

Senecio jacobaea is easily distinguished from other *Senecio* species in North America by its comparatively large size and highly dissected leaves. It most closely resembles *S. eremophilus* (Richards), but is clearly identified by the pattern of leaf dissection. The leaves of *S. eremophilus* taper to a point and are once-parted, whereas those of *S. jacobaea* are rounded and 2 - 3 parted (Frankton and Mulligan 1987).

Senecio jacobaea is also often confused with common tansy (*Tanacetum vulgare* L.), most likely due to the similarity in their common names. The two plants are similar in

height and leaf characteristics, but can be differentiated by *T. vulgare*'s discoid heads, phyllaries with dark margins, and strong odor.

Seed Biology and Fecundity

Tansy ragwort's high rate of seed production and development of two different forms of achenes contribute to this species' success as a weed. Also, the ability of both the root and the caudex to regenerate allows for vegetative reproduction, especially after disturbance.

Seeds of tansy ragwort do not show evidence of innate dormancy (Baker-Kratz and Maguire 1984), however, vegetation cover in the field may inhibit germination and dormancy may be induced by frost or drought (Meijden and Waals-Kooi 1979) or by burial (Thompson and Makepeace 1983). Meijden and Waals-Kooi (1979) observed that flowering is in part controlled by the attainment of a minimum rosette size with the probability of flowering positively correlated with rosette size.

Numerous insects visit the flower, mainly from the families of Hymenoptera and Diptera (Harper and Wood 1957). The flowers produce nectar and give off a faint odor. No conclusions have been drawn on the degree of self-compatibility.

Much variability exists among localities with regard to number of capitula and seeds (achenes) produced per plant (Wardle 1987). At their study site in New Zealand, Poole and Cairns (1940) reported that 1000 – 2500 capitula/ plant were produced per season and that each capitulum contained 55 seeds (achenes). In the U.K., Cameron (1935) found that individual plants produced between 68 and 2489 capitula and 70 seeds

per capitulum. Thompson (1980) found that seed production reached 15,000 – 25,000 seeds m^{-2} in peak years in New Zealand.

Dispersal

The flowering head opens when the expanding disc florets exert pressure on the involucre bracts. One may expect that tansy ragwort would be wind dispersed because the achenes have a pappus. However, Wardle (1987) concluded that it was a poor wind disperser. It was estimated that only 0.5% of the seeds produced were actually wind borne. Of the seeds released, 60% traveled only a few meters downwind (Poole and Cairns 1940). Seeds are dispersed via water or spread by livestock, either through ingestion or by being carried in the mud adhering to hooves (Schmidl 1972). Viable seed have been found in bird droppings (Bain 1991).

Each type of achene is adapted for a different habitat and mode of dispersal (McEvoy 1984b). The central disc achenes retain the pappus, have trichomes, and are lighter and more numerous than the peripheral ray achenes, which do not have a dispersal structure at maturity. McEvoy (1984b) suggested that tansy ragwort uses two separate strategies for colonization: 1) open disturbed habitats over a wide area, but including the home site, are colonized by disc achenes and 2) nearby, closed habitats may eventually be colonized by ray achenes.

Germination and Establishment

On the Oregon coast, tansy ragwort seeds mature in late summer and early fall. Maximum germination occurs relatively quickly at 18 and 21 days after flowering for

peripheral and central achenes, respectively (Baker-Kratz and Maguire 1984). There are two peaks of germination: fall and spring. However, some germination occurs year round (Harper and Wood 1957). The results of numerous studies unanimously agree that the viability of tansy ragwort seeds is high. Germination rates between 80 and 90% were achieved when seeds were subjected to alternating 12 h day/night periods with day/night temperatures of 30°/25° C and 60% germination rates for seeds produced by late flowering individuals (Schmidl 1972). Baker-Kratz and Maguire (1984) observed similar results overall in Washington. Wardle and Rahman (1987) found that achenes with the flower parts either abscised or removed were more viable than those with the perianth still attached.

Ideal germination temperatures are between 5 and 30° C (Meijden and Waals-Kooi 1979). Germination patterns were strongly correlated with variations in humidity at the soil surface, where desiccation of the soil inhibits germination (Sheldon 1974). Disturbance which brings seeds closer to the soil surface may break dormancy induced by burial. Both Meijden and Waals-Kooi (1979) and Poole and Cairns (1940) recorded higher germination rates among seeds buried 1 – 2 cm below the surface when compared with both those buried deeper and those on the soil surface. Thompson and Makepeace (1983) observed seeds to have a relatively high viability percentage (24%) after being buried for 6 years. Additionally, McEvoy (1984b) found that under similar conditions (20° C and 12 h light/dark), ray achenes were slower to germinate than disc achenes.

Both achene germination and seedling establishment in tansy ragwort are variable. Meijden and Waals-Kooi (1979) observed in the Netherlands that during the

same season, the percent germination rate of achenes produced by an individual in the field varied between less than 1 and 10%. They also found that survival of seedlings varied with habitat (from 2.2 to 8% in one season). The amount of pasture cover was found to significantly affect establishment. Meijden and Waals-Kooi (1979) found that surrounding vegetation affected seedling survival. In grassy areas few rosettes survived compared to cleared or woodland areas. The highest rates of survival and establishment were in cleared areas of grassland. They concluded that open habitats (soil and canopy) were most favorable to establishment.

Growth and Development

Once tansy ragwort is established, it is a good competitor at the rosette stage, since its leaves cover and suppress neighboring short plants such as grasses and clover (Harper 1958). McEvoy (1984a) observed that the death of a rosette provided an open site favoring germination of tansy ragwort. He found seedling establishment to be 4.3 times higher in openings left by ragwort plants that recently died than in immediately surrounding vegetated areas. Allelopathic effects of compounds produced by tansy ragwort, including the pyrrolidizine alkaloid jacobine (Wardle 1987), have been speculated, but no studies have evidenced such properties. Rosettes may grow to 30 cm in diameter under optimal conditions in the first season (Harper 1958). Vesicular-arbuscular mycorrhizal (VAM) associations have been observed from both European and United Kingdom (U.K.) populations (Hawker et al. 1957, Harley and Harley 1987), but similar associations have not been reported in North America.

In general tansy ragwort prefers mesic habitats. In Australia, tansy is found in high rainfall areas (Schmidl 1972) and in New Zealand it is found in areas where rainfall is greater than 870 mm yr^{-1} . Barkley (1978) described tansy ragwort to be established in areas with cool, wet, cloudy weather in North America.

Many different soil types have been found to support tansy ragwort, although it typically occurs on lighter, well-drained soils such as Podzolic grey loams or grey sands. Tansy ragwort is generally absent where the water table is high or the soil is very acidic (Meijden 1974).

Economic Significance

Tansy ragwort is of economic concern because the foliage contains pyrrolizidine alkaloids, which are toxic to cattle, deer, horses, and goats (Goeger et al. 1981, Giles 1983, Wardle 1987). Sheep are less affected by the alkaloids (Wardle 1987). The alkaloids accumulate in the animal's liver, and over time result in degradation of liver function and sometimes cancer. Species susceptibility appears to be correlated with the rate of production of pyrroles, a derivative of pyrrolizidine alkaloids, by the animal (Shull et al. 1976). Certain pyrrolizidine alkaloids have been shown to be carcinogenic, mutagenic and teratogenic (White et al. 1983).

Cattle do not generally graze tansy ragwort directly, except in severely overgrazed pastures. However, the alkaloids are still toxic in silage so the plant's presence in hay often results in the abandonment of the crop. The alkaloids also flaw honey produced by bees that have gathered ragwort pollen. The honey is usually too bitter and off-color to market (Deinzer et al. 1977).

Response to Management

The early phases of colonization are when tansy ragwort may be controlled most easily. Thus, early detection of tansy ragwort in new areas is important (Harper 1958). Common methods used to manage tansy ragwort include, chemical, mechanical, biological, and cultural practices. Dicamba (as Banvel®) at label concentrations was recommended by Whitson et al. (1985) for ragwort control with chemicals. Three significant problems confound the use of herbicides for tansy ragwort management. First, damage to competitive dicots by the herbicide is a common occurrence. Second, increased palatability of the weed to livestock just after spraying poses a threat to livestock health (Irvine et al. 1977). Livestock must be kept out of pastures for at least 3 – 4 weeks after spraying with herbicides in the spring. The third problem, is that studies have shown that herbicides were not effective in killing tansy ragwort plants because the herbicide leached out of the roots without being transported throughout the plant (Poole and Cairns 1940).

A single mowing during flowering might result in an increase in infestation levels because tansy ragwort is able to reproduce vegetatively. Conversely, repeated mowing may deplete nutritional reserves due to radical reduction in available photosynthetic tissue, thereby eventually causing the population to crash. Mowing may be effective if it is done every six weeks during spring and summer months and during a time of moisture stress (Cox and McEvoy 1983). Deep plowing has also been unsuccessful in controlling tansy ragwort because it tends to sever roots that can be the origin of new shoots and facilitate distribution over a wide area. Plowing also unearths buried seeds and thus can

contribute to increased infestation levels. Management techniques promoting dense vegetation in pastureland appear to be effective in controlling tansy ragwort spread, both because it does not readily establish from seed on closed canopy sites and because individuals are poor competitors during establishment (Thompson 1980). Hand pulling has been the most common mechanical management technique used on small areas in the early stages of infestation.

Three insects from tansy ragwort's native habitat have been introduced into the United States for use as biological control agents (Watt 1987a). The agents include the ragwort seedhead fly (*Botanophila seneciaella* Meade), the ragwort flea beetle (*Longitarsus jacobaea* Waterhouse) and the cinnabar moth (*Tyria jacobaea* L.). The seed fly larva feeds on the developing seeds and receptacle through the summer and can completely destroy the contents of a capitulum. The ragwort flea beetle adults feed externally on tansy ragwort foliage before entering summer diapause. The adults then resume feeding in the fall when conditions are cool and moist. Larvae feed internally on leaves, stem, and the root crown. Larval feeding often results in the killing of plants, and adult feeding can kill seedlings. The cinnabar moth larvae feed externally on the flowering shoots of tansy ragwort in spring and summer. The larvae are capable of completely stripping the shoots of flowers and leaves; however, this rarely kills the plant along the Pacific Coast, where fall rains regularly cause regrowth from the base of defoliated plants to occur (McEvoy et al. 1991).

Large decreases in tansy ragwort infestation levels have resulted with the introduction of these three biological control agents in western Oregon. At a study site

located along the central coast of Oregon, a 99.9% reduction in tansy ragwort standing crop was observed during an 8-year period following introduction of the three aforementioned insects. A decline of 93% was reported from a regional survey of 42 sites in western Oregon over 6 years.

The three biocontrol agents were released in northwestern Montana, beginning in 1997. In the area burned by the Little Wolf wildfire in 1994, the cinnabar moth decreased tansy ragwort infestation levels in the Flathead National Forest. However, the cinnabar moth has failed, so far, to establish despite repeated releases over three years. The seedhead fly has established in all parts of the main tansy infestation. The Oregon strain of the tansy ragwort flea beetle is still established in Montana five years after its initial release. The populations remain quite low, however, and have not moved beyond the release sites (Markin 2002).

Response to Burning

Early studies on tansy ragwort's response to burning are inconclusive. Poole and Cairns (1940) experimented with using a flame thrower to control tansy ragwort, but their results were inconclusive and have not been reproduced by others. Mastroguiseppe et al. (1982) conducted several control burns at an infested site in Redwood National Park, California, but those results were also inconclusive. However, observations in northwestern Montana indicate that tansy ragwort expands after wildfire.

The Final Environmental Impact Statement (FEIS) for the Tansy Ragwort Control Project for the Flathead National Forest in Montana cites that tansy ragwort was present in the Tally Lake Ranger District prior to the Little Wolf Fire in 1994 (Richardson 1997).

The FEIS states that in 1996, two years after the wildfire, a large population of tansy ragwort was discovered on the landscape. By late fall 1996, tansy ragwort infested approximately 1000 acres of national forest land, most of which had been burned by the Little Wolf Fire. The FEIS cites that the probable reason why a larger tansy ragwort population was not detected within the fire area in 1995 is that the new germinants were in the small rosette stage. The rosettes are relatively inconspicuous and may have escaped notice or proper identification as a noxious weed.

Justification for Research

Tansy Ragwort in Northwestern Montana

Management of weeds is often set in motion before monitoring is completed or even begun. Just as the weed can impact the ecosystem it has invaded (Mack et al. 2000), many management practices can have negative effects on the ecosystem. In some instances, it is quite obvious that the weed is increasing in density and/or spatial extent (i.e. invasive). However, the invasive plant may vary in invasion potential across different environments which can make management prioritization difficult. The purpose of my research was to quantify the invasiveness or potential for invasiveness of a new weed across environments where it has become established. I determined that conducting a population viability analysis would be the most effective method to quantify invasiveness of tansy ragwort.

Tansy ragwort was first discovered on the Flathead National Forest by a Tally Lake Ranger District forestry technician who conducted vegetation surveys in the Griffin

Creek drainage during the first week of August 1993. Peter Stickney, a forest ecologist with the USDA Intermountain Research Station, confirmed the discovery. Other surveys in 1993 confirmed the presence of more small "spot" infestations of tansy ragwort on the Tally Lake Ranger District. Tansy ragwort seeds may have been transported from Oregon on logging equipment used in site preparation within previously harvested units in these drainages, since four of the five populations discovered were located in harvest units that had been logged within the last ten years (Richardson 1997).

In 1994 several wildfires, most notably the Little Wolf wildfire, occurred in Northwestern Montana. The fire burned approximately 10,000 acres of the Tally Lake Ranger District in the Flathead National Forest and approximately 5,500 acres of the adjacent Kootenai National Forest. The following summers, populations of tansy ragwort were observed in the Flathead and Kootenai National Forests. U.S. Forest Service employees noticed that tansy ragwort colonized burned areas (Richardson 1997). These new populations were of particular concern due to use of the forest for cattle grazing and the related studies showing that tansy ragwort is poisonous to livestock and some wildlife (Goeger et al. 1981, Giles 1983, Wardle 1987). Tansy ragwort was also found in nearby unburned patches of forest and meadow. Only one other small tansy ragwort infestation is known in Montana, located on approximately twenty acres of private land in Mineral County near St. Regis in western Montana, west of Missoula (Richardson 1997).

The Montana tansy ragwort infestations are of particular significance because this species was thought to be limited to maritime climates. Montana sites were considered resistant to tansy ragwort invasion due to the prevailing low annual temperature, soil

moisture, and air humidity, which reduce tansy ragwort's capacity for germination. Soil drying has been shown to decrease tansy ragwort germination (Meijden and Waals-Kooi 1979). The sites in Montana infested with tansy ragwort are generally much higher in elevation and experience different climatic conditions than the coastal region and grassland sites previously invaded and studied in the Pacific Northwest region of North America. Previous studies in North America (McEvoy and Rudd 1993) that observed the effects of vegetation disturbance on tansy ragwort were conducted on sites that have cool and wet winters, but with ambient temperatures rarely falling below freezing; and where relative humidity is high compared to northwestern Montana. Winter temperatures in northwestern Montana frequently fall below freezing and the average annual precipitation of the infested area on the Kootenai National Forest is 57 cm (Table 1).

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Table 1. Climate data for the period of 1994 to 2002 for Libby 32 SSE, Montana weather station near Little Wolf Creek study site. Standard deviations are in parentheses. 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)
4.71 (1.00)	12.51 (1.38)	-3.09 (1.29)	56.36 (5.43)	264.60 (51.44)

The United States Forest Service (USFS) is the lead agency charged with the management of tansy ragwort in the infested national forest area of northwestern Montana. To develop ecologically based management strategies to reduce the spread and potential impact of tansy ragwort, it is important to examine the biotic and abiotic factors that influence tansy ragwort colonization and population dynamics in both burned and

unburned areas. Thus, I constructed a life history model for tansy ragwort and parameterized the model over a range of environmental conditions in northwestern Montana. The model describes the population dynamics of tansy ragwort plants in which the fecundity and mortality schedules have been calculated in relation to life-state. This approach provides managers with an instrument for quantifying the expected effects of natural or management-induced perturbations on tansy ragwort population dynamics in different environments. The model is an efficient means to estimate tansy ragwort invasiveness and subsequently prioritize populations for management across different environments. Modeling plant population dynamics is increasingly used for targeting weed vulnerabilities and predicting the effect of biological control organisms on the population size of the target weeds (Maxwell et al. 1988, Shea and Kelly 1998, McEvoy and Coombs 1999).

Primary Objectives for the Project

The primary objective of this project was to conduct a population viability analysis (PVA) including the construction of a life history model for tansy ragwort over a range of environmental conditions. PVA has been well developed for assessing threatened and endangered species but has not been widely used for invasive species. The PVA model is to serve as an exploratory tool for assessing the consequences of general forest management strategies, time, and natural perturbations on tansy ragwort population dynamics. My study also sought to identify the environmental conditions where tansy ragwort may be most invasive and therefore require management priority.

The specific environmental conditions we examined included: 1) areas burned by wildfire, 2) areas burned and logged, 3) undisturbed forest, and 4) undisturbed meadow.

Transition Matrix Models for Plant Populations

Weed control methods are usually focused on weed populations, therefore weed biology models should seek to estimate plant population behavior (Mortimer 1983). I approached the tansy ragwort field study by conducting a population viability analysis (PVA) including the parameterization of a transition matrix model over a range of environmental conditions. PVAs are typically based on matrix methods (Menges 2000).

Long term studies (Bradshaw 1981; Watt 1981; Davy and Jeffries 1981) have shown that in order to understand the abundance of plants it is necessary to understand the patterns of birth and death with age, the interactions with other organisms, and the effect of environmental variables, such as climate, on birth and death rates (Watkinson 1986).

Matrix models were first developed by Leslie (1945) and Lefkovich (1965) for animal population studies. The study of buttercups by Sarukhan and Gadgil (1974) first brought the use of matrix models to the attention of plant ecologists. These models are based on the realization that change in population size is not solely a function of population size, but depends on the structure of the population (Lotka 1925), which is the distribution of individuals in different life history stages, size classes, developmental, or functional stages (Sarukhan and Gadgil 1974). In the majority of plant populations,

reproduction is limited to one part of the year and to plants which have reached a minimum age or size.

Transition matrix models divide a plant population into age or size classes which have different rates of germination, reproduction, and mortality (Werner and Caswell 1977, Hubbell and Werner 1979, Abrahamson 1980, Silvertown 1982). Age structure has been incorporated into population dynamic models as age or stage class projection matrices (Leslie 1945, Sarukhan and Gadgil 1974, Mortimer 1983, Maxwell et al. 1988). States or stages may include seeds, various ages of plants, or definable developmental states, such as immature plants and reproductive plants. In matrix models, rather than a single number N_t for total population density, the numbers in each category or state are represented by a column vector (N_t) listing the numbers in each category. The survival probabilities for each state are summarized in a 'projection' or 'transition' matrix (Cousens and Mortimer 1995).

The life histories of many species can conveniently be presented in matrix form. The matrix can then be used to project the dynamics of the population (Caswell 1989). In particular, the dominant eigenvalue, λ , which is a measure of deterministic long-term population growth, and the elasticities (or proportional sensitivities) indicate the relative contributions of the matrix elements to the population growth rate (Cousens and Mortimer 1995). The fecundity of individual plants in the study can be related to all the potential explanatory variables (age, size, site, and year).

To project the number of individuals in each life stage, however, it is necessary to assume a stable age distribution. Two assumptions must be made when using matrix

models to forecast population growth: 1) that the age-specific survival rates have remained the same from year to year, so the probability of survival from one age class to the next is the same as would have been obtained if a single cohort had been followed through time, and 2) that recruitment into the population is constant from year to year (Watkinson 1986). We overcame these two constraints by calculating the population growth rate (λ) at the point (generation) where the proportion of mature plants became stable.

Transition Matrix Models as a Tool

Transition matrix models give insight into population dynamics which cannot be obtained from simple continuous models of population growth. The use of transition matrix models and population viability analysis to facilitate the study of plant populations has its origins in conservation biology. Both weed science and conservation biology studies often include variables related to site manipulation and metapopulation level processes. Thus, it is appropriate that weed science look to conservation biology for techniques to assist study of the biology of weeds and particularly to assess population potential to become invasive and subsequently to assess management practices.

Models can provide insight and an understanding of the interaction between an invasive plant and its environment that may help the development of theory, formulation of hypotheses and more practically, are useful in prioritizing land management objectives. Sarukhan and Gadgil (1974) were able to show relationships between the degree of stability of the population and the importance of seed to the plant species rather than vegetative reproduction. They did this by expanding the matrix method to include

vegetative reproduction. Although Sarukhan and Gadgil used a buttercup species, not a weed, their study is useful for managing weeds because it shows how the matrix method can be used to identify limiting life history stages.

Drayton and Primack (1999) tested the hypothesis commonly assumed in weed science and conservation biology, that small populations are more vulnerable to elimination and extinction than large populations. By comparing control populations of the biennial weed garlic mustard (*Alliaria petiolata*) with experimental populations, they found 43% of small populations were more susceptible to extinction than large populations. Their results and simple population model suggest the importance of buried seeds in allowing garlic mustard to persist despite attempts to eradicate the weed.

Shea and Kelly (1998) used a matrix model to assess the impact of biological control and other pest management strategies. They constructed a simple, single-species, stage-structured model (transition matrix model) for the invasive plant species, nodding thistle (*Carduus nutans*). They confirmed with the matrix models that populations at two sites were increasing in number. An elasticity analysis also showed that the seed/seedling and small-plant/seed transitions were the most important (the "Achilles heel") to population growth.

Neubert and Caswell (2000) used a population model to calculate invasion speed using data from the plants teasel (*Dipsacus sylvestris*) and *Calathea ovandensis*. They define invasion speed as the speed at which the geographic range of the population expands. They demonstrated how to compute the sensitivity and elasticity of invasion wave speed for both demographic and dispersal parameters. They accomplished this with

the construction of a discrete-time model for biological invasions that coupled matrix population models with integrodifference equations, and then derived formulas for the sensitivity and elasticity.

The influence of vital rates or matrix elements on population growth rate may be measured with perturbation analyses (sensitivity and elasticity analyses). Zuidema and Franco (2001) applied variance-standardized perturbation analysis to six plant species with different life histories. They calculated population growth rates (λ) for each simulation by drawing 1500 random values from observed frequency distributions of each vital rate in each size category. The product of sensitivity (or elasticity) and degree of variability of a vital rate was a good estimator of the variation in λ , accounting for 95% of the variation in λ in the six species. Their results support the use of variance-standardized perturbation analyses to determine the impact of vital rate variation on population growth rate.

Transition matrix models are often used in conservation biology to evaluate the effects of environmental stochasticity and different management methods. Lennartsson and Oostermeijer (2001) utilized the biennial *Gentianella campestris* to compare the effects of traditional grassland management with continuous summer grazing in Scandinavian grasslands. They concluded that traditional management is more favorable for *G. campestris* and that lambda values may be underestimated due to the occurrence of drought in one out of five summers during the study period.

PVA

A prevailing concern when monitoring plant population dynamics is accuracy in capturing and modeling variability in population demographic processes across environmental gradients. PVA is used to assess population persistence based on a combination of empirical data and modeling scenarios. PVA uses life history or population growth rate data to parameterize a population model, which is then used to project and estimate future population size and structure. A PVA includes empirical data on the entire life cycle of a wild population and uses quantitative modeling to forecast future population dynamics. Specifically, PVA seeks to measure the finite rate of increase (λ), extinction probability, time to extinction, and/or future population size or structure (Menges 2000). The majority of PVAs utilize matrix modeling methods as discussed in the previous section. PVA is used both in animal and plant biological experiments. In contrast to animal PVAs, most plant PVAs are based on stage- or size-classified matrices.

PVA is used for a variety of reasons including predicting the future size of a population, estimating the extinction probability over time, assessing the influence of certain management methods, and investigating the consequences of different assumptions on population dynamics (Coulson et al. 2001). To conduct a proper PVA, a model must be selected or constructed that includes the important aspects of the species' life history. PVA models can be quantitative and mathematically challenging, or simple qualitative models. The majority of PVA models include demographic and/ or genetic components of risk.

Traditionally PVA is used to monitor the population growth rate of endangered plant species, but PVA can also be applied to invasive plant ecology to quantify the invasiveness of a plant species. Using the criteria outlined by Rejmanek et al. (2002) I define an invasive plant as a non-indigenous plant species that is increasing in density and/or spatial extent. Invasive does not imply that a population or metapopulation has an impact on the ecosystem. A weed is defined as a subset of plant species, not necessarily a non-indigenous species, placed on a list (often by law) based on a professional consensus that the species represents some problem for people.

Many parallels exist between conservation biology and invasion biology. The urgency of the issues that biologists from both disciplines must address is one obvious parallel. Whether dealing with an endangered species or an invasive species threatening the viability of native species, there is rarely time to assess a situation extensively before managers must act.

In a paper discussing issues related to PVA, Reed et al. (2002) suggest restricting the definition of PVA to development of a formal quantitative model. They also designate the most appropriate use of PVA for comparing the relative effects of potential management actions on population growth or persistence. Our objective was to use PVA in combination with the life history model as a first approximation comparison to assess the potential (invasiveness) of tansy ragwort in different environments. Given this non-traditional use of PVA and the differing views on the most appropriate use of PVA, we consider how invasive plant ecology fits within the scope of PVA.

Concerns in Conducting PVA in Invasive Plant Ecology

From the time of its introduction, PVA has been generally thought of as the most objective method for quantifying the viability of natural-occurring populations (Harting 2002). Scientists have raised concerns regarding the limitations of PVA as related to endangered-species monitoring. The limitations associated with using PVA to assess extinction risk gives one insight into the possible limitations of using PVA to assess invasiveness. Concerns frequently voiced in endangered species literature (Harting 2002) led us to outline five concerns related to using PVA to monitor invasive plant species:

1. Reduced predictive precision due to the abbreviated time series of data available
2. Uncertainties regarding the value of λ for estimating invasiveness.
3. Inability to anticipate environmental stochasticity/variability.
4. Lack of prior knowledge of the ecology of the invasive plant in its new environment.
5. Uncertainties regarding the inference space of invasive plant population models and their limited parameterization.

Short Time Series of Data. PVA with a model depends on the structure of the model and quality of the data (Harting 2002, Reed et al. 2002). Often in the real world, it is a luxury to have ample funding and time to collect quantitative data on which to base management decisions. In the case of endangered species, a sense of urgency arises out of the thought that the species is going towards extinction and the unknown time frame in which managers have to act. In the case of invasive species, land managers are often under pressure to do something about the invasive plant population. Biologists

compensate for lack of data by relying on theoretical techniques and empirical generalizations (Doak and Mills 1994).

The median length of study for plant PVA is only 4 years (Menges 2000). Gathering a thorough spectrum of data on plants is a difficult task in such short-term studies. PVAs for plants are limited by sufficient data for certain parts of the plants' life cycle. For example, both plant and seed dormancy and periodic recruitment presents problems for biologists with only a short amount of time to gather empirical data. Mortality estimates are likely to be inflated in short-term studies involving dormant individuals (Lesica and Steele 1994). Further, seed bank dynamics can contribute significantly to population growth, resulting in the case of conservation, in extinction avoidance, or in invasion ecology, in species persistence. Yet, data on seed dormancy and seed banks are often incomplete (Menges 2000).

Periodic recruitment, characteristic of several species and habitats, is also problematic in short-term studies. Menges and Dolan (1998) were able to model episodic seedling recruitment in royal catchfly (*Silene regia*) using matrices representing recruitment and nonrecruitment years.

It is important to account for imprecision in parameter estimates and its consequences for risk assessment (Ellner et al. 2002). Various methods for testing PVA predictions with field data are reviewed by McCarthy and Broome (2000) and McCarthy et al. (2001). Modern statistical practice require that every statistical estimate be accompanied by a measure of its precision if inferences are to be drawn from the estimates (Sokal and Rohlf 1981). Confidence intervals may be obtained from

simulations for complicated models used in PVAs (Ellner et al. 2002). For some models, confidence intervals can be obtained by repeatedly resampling and fitting real data (Sokal and Rohlf 1981).

Value of λ for Estimating Invasiveness. When modeling plant population dynamics, biologists ask what types of population density trajectories are plausible. The 'path' which population density follows over time is referred to as its trajectory (Cousens and Mortimer 1995). In both endangered species and invasive species management, the direction of change in population density is of particular interest. The rate of change in populations (λ) is also of interest. This rate determines when a species will go extinct, (an issue in conservation) or become invasive, (an issue in invasion ecology).

The main objective in population dynamics studies is to understand the implications of observational experimental data in order to forecast population trajectories. With this knowledge, management changes can be made to influence a decrease or increase in abundance. Through monitoring, researchers may be able to retrospectively identify certain events which coincide with changes in trajectory (Cousens and Mortimer 1995). In addition, data on causes of change can be collected objectively from experiments by systematically varying causal factors.

If a habitat has the necessary resources for the species to grow and reproduce, and is large enough to support an expanding population, then the species may increase in abundance. The species' rate of change (λ), or its multiplication rate, is the ratio of population size in successive generations where population sizes are measured at a common point in the life cycle (Cousens and Mortimer 1995). The general rule of thumb

defines an increasing plant population to have a $\lambda > 1.0$. If plant survival and reproduction become reduced, one would expect λ to decrease ($\lambda < 1.0$). If a given population increases through reproduction and then the increased abundance is subsequently cancelled out by increased mortality, then population density would remain constant, and the population could be referred to as locally stable ($\lambda = 1.0$).

The question then becomes what types of population trajectories occur in reality? Neither graphical nor mathematical models are of practical use unless they can accurately capture the spectrum of real trends in population dynamics. The lack of long-term data sets further increases the likelihood of inaccurate characterization of population trends. Stochasticity, introduced through changes in management practices or climatic perturbation may cause long or short-term oscillations in population density, making it difficult to identify true trends (Cousens and Mortimer 1995). One must question whether the arbitrary threshold of $\lambda = 1.0$ accurately indicates population decline, increase, or equilibrium with so many extraneous factors affecting population density.

Conservation ecologists suggest de-emphasizing the exact values of λ and extinction probabilities in order to avoid some of the problems of uncertainty in demographic parameters (Menges 2000). Beissinger and Westphal (1998) recommend that PVA examine relative rather than absolute extinction risk, that projections be made only over short time periods, and that simple models be used preferentially over more complex ones (Okum's razor). This approach may be especially useful when comparing alternative management strategies. For example, Menges and Dolan (1998) compared λ s and extinction probabilities for royal catchfly (*Silene regia*) among three groups of

populations with contrasting management regimes. These concerns would logically transfer to invasion ecology.

Inability to Anticipate Environmental Stochasticity. Environmental stochasticity is the variation in demographic parameters caused by environmental (competitors, disease, disturbance, etc.) variation affecting whole populations (Menges 2000). Increasing environmental stochasticity usually means increasing extinction risk, and could also increase mistakes in identifying invasiveness in plant ecology. Given the lack of adequate time to collect complete data, biologists are often concerned about capturing enough data over time and/ or space to accurately model and interpolate environmental variation. Many approaches exist to include environmental stochasticity in models.

Due to reduced size of data sets and the inherent computational simplicity of this approach, stochastic analyses assume first, that matrix elements are not correlated, and secondly, that there is no autocorrelation over time. Yet, demographic parameters are usually positively correlated across environments (Horvitz and Schemske 1998) and sometimes over time, as in the Markov process. This positive correlation causes more extreme year-to-year outcomes and prediction of larger extinction risks (Nakaoka 1996) and assumably would cause overestimation of invasiveness.

A popular approach used by ecologists concerned with predicting risk of extinction is to retain elements within the original matrix and select these matrices probabilistically over time to incorporate the effects of environmental stochasticity into the model (Menges 1990). This matrix selection approach preserves correlation structure and yields a conservative risk assessment versus allowing matrix elements to vary

independently. Menges (2000) suggests that ecologists should collect data that quantifies the correlation structures among matrix elements and among populations, because these affect extinction risks. He concludes that in the absence of data, modeling the effects of correlation structure on extinction risk may help determine conservative risk assessments.

Calculation of stochastic population growth rates has become more common. The advantage of stochastic λ s over deterministic λ s is that they are not attached to a particular time frame (as are extinction probabilities). Therefore, they can be compared across studies and they give a more conservative risk assessment than λ s calculated from mean matrices for species in erratic environments (Menges 2000). Lastly, including more specific data of different types of variation (i.e., successional, disturbance, spatial, and temporal environmental effects, etc.) in models will increase the accuracy and precision of forecasting persistence.

Alternatively, in invasion ecology, to decrease the risk of not concluding that a species is invasive when in fact it is, demographic parameter values should be selected from empirical distributions to maximize the variance in λ estimates. This strategy is less conservative if predicting potential invasiveness by decreasing the potential for a type two error.

Lack of Prior Knowledge of the Ecology of the Invasive Plant. Proper PVAs are based on life history models, often transition matrix models, which capture the important aspects of a species life history. In this case, the model must take into account all available data and consider the salient dynamic processes that influence the long-term persistence of the population.

In the case of endangered species, uncertainty is dealt with through risk analysis by calculating the probabilities of persistence (Reed et al. 2002). As Mack et al. (2000) explain, when non-native organisms are transported to new regions, at first many and often most of the organisms do not survive. The authors speculate based upon the number of species observed only once far from their native range, that local extinction of immigrants shortly after their arrival must be high. However, some naturalized species do succeed and become invasive in their new environment. Immigrants may succeed due to: escape from natural predators, vacant niches including resource fluctuation, and disturbances that disrupt native communities (Simberloff 1981). Invasive plants can drastically alter ecological processes such as fire regime, hydrology, nutrient cycling, and energy flow in a native system posing new difficulties to researchers trying to model them because assumptions once held about plant population dynamics may not apply in such an altered ecosystem (Mack et al. 2000). When insufficient information impedes satisfactory estimates of such effects (including intra- and inter-specific density dependence), researchers may be limited to discussing the potential for growth of a population of the non-native plant in its invasion phase.

Inference Space. In the case of invasion ecology, the majority of uncertainty lies in the lack of information about how invaders can alter fundamental ecological properties. Lack of ecological information on the invasive plant, is the problem of uncertainties in inference space. Researchers may collect data about a species in habitats of one geographic location, and often projections are extrapolated to different habitats or regions of the world. Populations for example, may be small because of unfavorable site

conditions, thus confounding implications of population size with those of environmental quality (Drayton and Primack 1999).

A metapopulation is a group of interacting populations (Menges 2000).

Metapopulation approaches may be relevant to understanding persistence in plants because many plant species have patchy distributions and occur on specialized sites.

Patchiness may also be created by disturbance or dispersal mechanisms. Knowledge of the species location and ability to predict susceptible habitats is integral to a strategy of weed management (Cousens and Mortimer 1995).

Summary

Technological advances in computer programming and thus modeling have made tools such as PVA more accessible to ecologists. As more field data is collected on invasive plant species, PVA may prove to be an insightful approach to understanding invasive plant species population dynamics and the environments in which they invade. The concerns raised here were drawn partly from conservation biologists' experience with PVA and partly from problems unique to invasive plant ecology. The relatively new science of invasive plant ecology can benefit from the experience and toolbox of conservation biology. The environments invaded by tansy ragwort in northwestern Montana provided distinct areas between which to compare tansy ragwort population dynamics. The tansy ragwort model and PVA will serve as a case study attesting to the kind of information that can be quantified using PVA and how it may help prioritize land management.

THE EFFECTS OF ENVIRONMENT ON TANSY RAGWORT (*SENECIO*
JACOBAEA) POPULATION DYNAMICS

Introduction

Increasingly, invasive species have become an important component of conservation-related issue. Invasive plants may alter ecosystem properties and processes (Mack et al. 2000) and native community structure (Simberloff 1981). They may also threaten remnant protected plant species within conservation reserves (Usher 1988). Understanding invasive species' population dynamics is important to increasing efficacy of management methods.

Tansy ragwort, a noxious weed (Agriculture 2003), was introduced to North America from Europe. In addition to displacing native desirable plants, tansy ragwort is poisonous to livestock and some wildlife (Deinzer et al. 1977, Goeger et al. 1981, Giles 1983). Invasive populations of tansy ragwort were previously thought only to occur in maritime environments in North America. However, tansy ragwort established and has been observed by land managers to be spreading at sites in northwestern Montana and adjacent northern Idaho.

In Montana, tansy ragwort attained noxious weed status after colonizing areas burned in the northwestern region of the state in a 1994 wildfire. Northern Rocky Mountain wildfires of 2000 and 2001 produced large areas thought by land managers to have potential for colonization by tansy ragwort. It is important, therefore, to understand biotic and abiotic factors influencing tansy ragwort colonization and population dynamics

in burned and unburned areas. This field study was designed to parameterize a transition matrix model to evaluate the effects of four different environments on the population dynamics of tansy ragwort in northwestern Montana.

In conservation studies, when knowledge gaps exist due to lack of biological data on species, researchers turn to ecological theory to aid in the design of species management plans (Doak and Mills 1994, Kareiva 1994). When a species is thought to be tending toward extinction, conservation biologists use empirical data in combination with models to predict how natural perturbations and management actions will affect the population's extinction risk and/or population growth rate. Likewise, in invasion ecology, models have helped bridge the gap between the field and the laboratory or greenhouse (Hilborn and Mangel 1997).

Models of plant population dynamics are increasingly used to target weed vulnerabilities and to predict the impact of biological control organisms on the abundance of target weeds (Maxwell et al. 1988, Shea and Kelly 1998, McEvoy and Coombs 1999). Transition matrix models provide insight into population dynamics which cannot be inferred from continuous models of population growth. Conservation biologists have made use of transition matrix models for population viability analysis to facilitate the study of plant populations at risk for extinction. Both conservation biology and weed science studies often include variables related to site manipulation and metapopulation level processes. Thus, it is appropriate for invasion ecologists to borrow from conservation biology techniques both to assist in the study of invasive plant biology and to assess management practices.

Models can provide an understanding of the interaction between an invasive plant and its environment then assist in the development of theory, formulation of hypotheses and more practically, land management priorities. Sarukhan and Gadgil (1974) were able to show the relationship between the degree of population stability and the mode of reproduction in a buttercup species, highlighting the importance of seed over vegetative reproduction. They accomplished this comparison by expanding their matrix method to include vegetative reproduction.

Maxwell et al. (1988) developed a population model for leafy spurge (*Euphorbia esula*). Using a model parameterized with field data and employing sensitivity analysis, they were able to demonstrate that transition from basal buds to vegetative shoots, survival of vegetative shoots, and survival of basal buds over winter were all important transition parameters influencing population growth. They also used the model to simulate four control strategies and compared population response with actual field studies which allowed them to generate correlations evaluating model response with field results.

In another study by Maxwell et al. (1993) a population model was developed for salmonberry (*Rubus spectabilis* Pursh) and thimbleberry (*Rubus parviflorus* Nutt.). This study is an example of how phenological, environmental, and intraspecific density effects may be incorporated into a species-specific model to simulate their effect on demographic processes.

Shea and Kelly (1998) used matrix models to assess the impact of biological control and other pest management strategies. They constructed a transition matrix

model for the invasive plant species, nodding thistle (*Carduus nutans*) in New Zealand. Their work is an example of the use of a simple, single-species, stage-structured model in invasive plant control. They confirmed with the matrix models that populations at two different sites were increasing. An elasticity analysis also showed that the seed/seedling and small-plant/seed transitions were the most important (the "Achilles heel") to population growth.

Neubert and Caswell (2000) used a population model to calculate invasion speed using data from the plants teasel (*Dipsacus sylvestris*) and *Calathea ovandensis*. They defined invasion speed as the speed at which the geographic range of the population expands. They demonstrated how to compute the sensitivity and elasticity of invasion wave speed to both demographic and dispersal parameters. They did this with the construction of a discrete-time model for biological invasions that coupled matrix population models with integrodifference equations and then derived formulas for sensitivity and elasticity.

I conducted a population viability analysis including construction of a life history model for tansy ragwort over a range of environmental conditions including: 1) areas burned by wildfire, 2) areas burned and then salvage-logged, 3) undisturbed forest, and 4) undisturbed meadow. Here I report the results from the first two years of a four-year study. Hypotheses tested were associated with each vital rate for each environment compared with the vital rate calculated for the populations in the unburned-unforested areas as a control. Our null hypothesis was that tansy ragwort population growth rates (λ) would not differ between environments.

The primary goal of my research was to determine under which environmental conditions in northwest Montana tansy ragwort is invasive ($\lambda > 1.0$) thus creating a profile of areas that should be prioritized for management. A secondary goal was to determine which demographic processes contribute most to invasiveness so that those processes would be targeted to optimize management efforts. The specific objectives were:

1. To calculate transition rates between tansy ragwort population life history states,
2. To compare the median transition rates estimated for four different environments (burned by wildfire, burned by wildfire followed by logging, forest not burned and natural meadow not burned),
3. To test transition rates for density dependence,
4. To use the full spectrum of transition rates in a Monte Carlo simulation model to forecast population dynamics and compare population growth rates (λ_s) for each environment,
5. To use model parameter perturbation/elasticity analysis to identify transitions (demographic processes) that are proportionally most significant in regulating population size, and
6. To quantify the relationship between specific environmental variables including soil characteristics and the transitions found to be most important in elasticity analysis.

Materials and Methods

Site Description

The field study was performed approximately 60 miles southeast of Libby, MT in the northwestern part of the state. Areas with different histories of disturbance were identified in June 2001. One region was selected for study on the Kootenai National Forest in the Little Wolf Creek drainage in northwestern Montana where patches of forest

stands were burned by the Little Wolf wildfire of 1994. Sites with patches of tansy ragwort were selected on south- to west-facing slopes with vegetation habitat types varying from forest to grassland types (Pfister et al. 1977). Four forested burned and salvage-logged sites and four burned sites with no salvage-logging following the fire were initially selected. Due to the large area of the Little Wolf wildfire and limited accessibility, only one unburned-forested area (forest) and one unburned-nonforested area (meadow) could be located for sampling in proximity to the other sites. The forest and meadow sites were found where roads crossed a slope and acted as a fire break, resulting in an undisturbed island of forest and meadow in the center of the burned area. Physical characteristics for all 10 study sites are summarized in Table 2. One of the ten sites is located on land owned by the Plum Creek timber harvesting company and the remaining nine sites are located on the Kootenai National Forest (KNF).

Table 2. Selected site characteristics for all 10 study sites in the Kootenai National Forest.

Environment ^a	Biocontrol release site ^b (km)	Elevation (m)	Aspect	Slope (degrees)	Canopy cover (%)	Habitat type ^c
BSL	1.61	1183	S-SW	14	0 - 3	ABLA/ CLUN
BSL	1.61	1229	SW	16	3	PICO/CARU
BSL	2.25	1480	S-SW	7	0	ABGR/XETE
BSL	0.4	1702	S-SW	12-15	0	ABGR/XETE
B	1.61	1218	SW	5	5	ABGR/ CLUN
B	1.61	1225	SW	5	3	PICO/CARU
B	2.25	1475	S-SW	20	0-3	PICO/LIBO
B	0.16	1705	SW	24	5-10	ABGR/XETE
Forest	3.22	1680	S	2-5	35-40	ABLA/ CACA, GATR phase
Meadow	2.41	1224	S-SW	3	0	FEID/DECE

^a BSL, burned and salvage-logged; B, burned; F, Forest; M, Meadow

^b Distance to nearest insect biological control agent release site

^c 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 average annual precipitation of the infested area on the Kootenai National Forest from 1994 to 2002 was 57 cm and the average annual temperature was 4.71 °C. The soils in the study site are Andic Dystric Eutrochrepts, fine-silty, mixed, frigid loam (Kuennen and Nielsen-Gerhardt 1995). Summer cattle-grazing allotments exist on the KNF; however, following the Little Wolf wildfire in 1994, the burned area has been closed to grazing. Therefore, none of our ten study sites had been grazed by cattle since before 1994.

The population viability analysis was restricted to ten 1m² plots at each site (environment) except in the meadow site where only five sample populations could be

located. Due to the characteristic spate distribution and density of tansy ragwort infestations, the adaptive sampling method was followed to locate the position of each sample population at each site (Thompson 2002). This method is designed for aggregated and low frequency populations. In nine of ten sampling sites, a 100 m transect was established through areas where tansy ragwort populations occurred. Each 1 m² sample plot was installed perpendicular to the 100 m transect at each of ten randomly located positions where tansy ragwort plants were encountered. In the meadow study site, sample plots were installed in all five of the patches found in that environment. A 1 m² wire frame with 1/16 m² grid was used to overlay each plot to census individual tansy ragwort plants in late May/early June and late August of 2001 and 2002.

In addition to physical features and some general vegetation measures at each site (Table 2), topographic position, distance from road, and distance from biocontrol release site were also measured at all sites. Plant species located within a 20 m x 20 m area containing the sample population were also recorded. Other environmental measurements included mapping of abiotic features (rocks, logs, bare soil) in each sample plot.

Transition Rates

To quantify transition rates between tansy ragwort population life history states (Objective 1), I mapped individual plants in each of the environments. I followed the fate of all tansy ragwort individuals occurring in each of the 1 m² sample plots. Individuals were categorized according to classes in the life-cycle model (Figure 2). Classes recorded at each population census include seed bank (estimated from seed produced),

seed produced, seedlings, rosettes, and flowering plants. Plants were considered seedlings if they had five leaves or less, rosettes were distinguished by having 6 or more leaves and flowering plants had bolted stems bearing flowers.

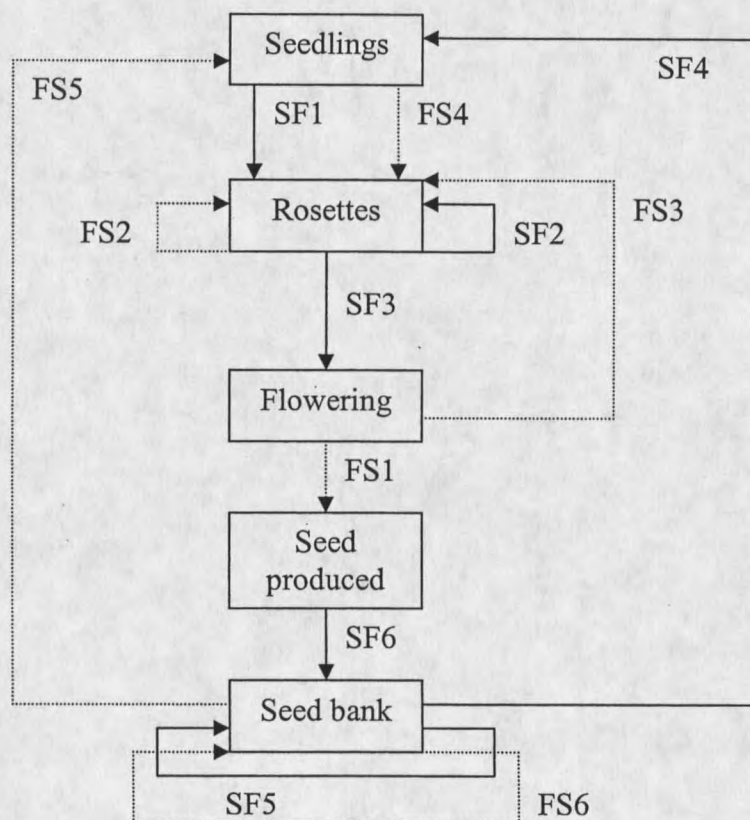


Figure 2. Life-cycle model for tansy ragwort. The life history stages (states) are in squares and the arrows indicate all possible transitions. Solid arrows labeled SF indicate spring to fall transitions; dashed arrows labeled FS indicate fall to spring transitions.

The life-cycle for tansy ragwort (Figure 2) was translated into two projection matrices, a spring-to-fall transition matrix and a fall-to-spring transition matrix. Each tansy ragwort stem in the square meter sample plot was first mapped on a piece of graph

paper corresponding to the $1/16 \text{ m}^2$ grid overlaying the plot. Subsequent stem (seedlings, rosettes, flowering shoots) censuses were mapped on acetate paper overlaying the original graph paper map. Transparent maps allowed me to keep track of individual stems except when the seedling density was very high. Identity of surviving seedlings was not required for the transition probability for seedlings entering the rosette class (Table 3). A seedling surviving from one census to the next by definition became a rosette.

Table 3. Tansy ragwort life stage transitions, how they were calculated, and explanation of the abbreviations.

Transition	Calculation	Where:
SF1	$\text{sdltorossf}_{\text{fall } t+1} / \text{sdl}_{\text{spring } t}$	sdltorossf = number of seedlings that transitioned to rosettes from the spring census to the fall census, sdl = number of seedlings, t = year 2001
FS4	$\text{sdltorosfs}_{\text{spring } t+1} / \text{sdl}_{\text{fall } t}$	sdltorosfs = number of seedlings that transitioned to rosettes from the fall census to the spring census (over winter).
SF2	$\text{rostorossf}_{\text{fall } t} / \text{ros}_{\text{spring } t}$	rostorossf = number of rosettes that remained rosettes from the spring census to the fall census, ros = number of rosettes
FS2	$\text{rostorosfs}_{\text{spring } t+1} / (\text{sdltorossf}_{\text{fall } t} + \text{rostorossf}_{\text{fall } t})$	rostorosfs = number of rosettes that remained rosettes from the fall census to the spring census
SF3	$\text{rostoflwsf}_{\text{fall } t} / \text{ros}_{\text{spring } t}$	rostoflwsf = number of rosettes that transitioned to flowering shoots from the spring census to the fall census
FS3	$\text{flwtorosfs}_{\text{spring } t+1} / \text{rostoflwsf}_{\text{fall } t}$	flwtorosfs = number of flowering plants that reverted to rosettes from the fall census to the spring census

Seed Production

To quantify the transition rate from flowering shoots to seed produced (FS1), the number of seeds produced per plant was estimated annually by randomly selecting flowering plants per study site in the fall census (late August). The randomly selected plants were clipped, brought back to the laboratory in Bozeman, dried, and the seeds per plant were counted (fecundity) for flowering plants. This measurement is directly related to fecundity, because only flowering plants produce dispersing propagules (achenes).

The seeds taken from the sampled plots for counting were not returned to the plots. Therefore, to compensate for the lost seed, the seed survival rate (SF5 and FS6) was increased by the proportion of seed taken in those plots that were sampled for seed production. If adding that proportion to the survival rate caused a number larger than 1.0 then I chose to set the probability to 0.8, which was the approximate viability of the seed before the seed burial experiment described in the following section.

Seed Bank

To quantify seed survival rate in the soil seed bank, tansy ragwort seeds were buried at each of the ten study sites. Six fine nylon mesh bags were buried 2 cm below the soil surface at each site in October 2001. Each bag contained 200 seeds. Two bags of seeds (400 seeds) were unearthed in August 2002. Plans include unearthing two more bags in August 2003 and the final two bags in August 2004. A sample of 300 of the original 2001 dried seed has been stored in a paper bag in a laboratory drawer since October 2001. The viability of 100 of these seeds was tested in August 2002. The

viability of the remaining 200 seeds will be tested annually for the next two years (100 seeds/ year) of the experiment.

In the laboratory, the seeds from the field were emptied from the nylon bags and counted. If less than 200 seeds were found remaining in the bags, it was assumed that the seeds missing were lost to decay, germination, or possibly predation by beetles. The unearthed and the stored seeds were placed on moist blotting paper in clear plastic boxes and left overnight to imbibe. After imbibition, with the aid of a magnifying lens, each seed was nicked with a razor blade at the cotyledon end. The nicked seeds were then placed in a small petri dish with 1% tetrazolium solution and left at room temperature overnight. The following morning, the tetrazolium-treated seeds were inspected under a microscope for color change. Seeds with red-stained embryos were considered viable whereas white to patchily-stained embryos were considered not viable.

The seed bank to seedling transition (emergence rate) was calculated for each 1 m² plot as follows for the spring to fall transition (SF4):

$$\text{seedlings}_{\text{fall } t+1} / (\text{seed produced}_{\text{fall } t} * \text{mean seed survival rate}_{\text{environment type}});$$

and for the fall to spring transition (FS5):

$$\text{seedlings}_{\text{spring } t+1} / (\text{seed produced}_{\text{fall } t} * \text{mean seed survival rate}_{\text{environment type}}),$$

where t = year 2001.

My model assumed that seed quality was equal among individuals, meaning each seed produced was at least 80% viable and equally capable of germination. The number of emerging seedlings was divided by the number of seeds produced by individuals in the flowering plant stage class from the previous census, then multiplied by the mean seed

survival rate for seeds buried in the respective environment type. Annual seedling emergence was assessed in all 95 demographic plots. I assumed that all seeds produced in year t (2001) survived to year $t + 1$ (2002), by entering the seed bank; by extension, immigration was assumed to be equal to emigration with a transition rate (SF6) equal to 1.0. Thus a proportion of the seed bank produced seedlings. The seed survival rate of the four subsamples of seeds taken from the two unearthed nylon bags per environment were randomly chosen as the seed bank to seed bank (SF5 and FS6) transition elements of the matrices.

Another approach was taken to estimate the proportions of seedlings emerging from the soil seed bank using a controlled field experiment. Four hundred seeds were sown in each of four 0.25 m² rings in the Little Wolf wildfire study area in the spring of 2001. The seeds were collected from randomly sampled mother plants in the Burned and Salvage-logged, Burned, Forest, and Meadow sites in fall 2000. The emergence of the year 2000 cohort was monitored weekly from June to August 2001 and again in May 2002 and August 2002. The number of seedlings per plot from this sowing experiment in the year 2001 was taken as the emergence rate from the seed bank (SF4) for the spring to fall transition matrix for the second simulation of the tansy ragwort model.

The fate of seeds (seed bank and seed produced) from fall year t (2001) to spring year $t + 1$ (2002) reflects germination and establishment of seedlings and rosettes. For the seed bank to seedling transitions (SF4 and FS5), fall 2001 seed produced values were used in the 2001 transition matrices, because there was no data for fall 2000. The fate of rosettes reflects the winter survival of rosettes and the performance of adult plants

(rosettes and flowering plants) in year $t + 1$ (2002). Finally, the fate of adults reflects the production of seeds in year t (2001), and the germination and establishment of seeds in year $t + 1$ (2002).

Once transition rates were calculated per 1 m² plot, the median transition rates were calculated for each set of plots (populations) in each environment type. To meet objective 2, median transition rates were qualitatively compared for the four different environments using box and whisker plots which included the median and 95% confidence intervals for the median transition rates.

Density Dependence

Density dependence is one of the most common population regulating mechanisms invoked to make population models more realistic. However, there is inconsistent empirical evidence for its influence on specific demographic processes. Intra-specific density-dependence was investigated (Objective 3) using simple linear regression, where the relationship between reproduction and mature plant density was tested. Seed produced per plant and transition from flowering shoots to vegetative shoots (vegetative reproduction) were regressed against mature plant density. Inter-specific density-dependence was investigated using simple linear regression, where the relationships between tansy ragwort fecundity, vegetative reproduction, and population growth rate were tested against percent cover of other species in each plot.

Population Growth Rates

To take full advantage of the demographic rates calculated for each plot, transition values were inserted into the transition matrices of the model (Table 4) to simulate population growth in the different environments. Thus, objective 4, comparing population growth rates (λ) for the different environments, was fulfilled by iteratively selecting plot-specific transition rates, simulating population dynamics for 100 generations, and calculating population growth (λ) based on changes in rosette plus flowering shoot density in the fall of each generation.

Table 4. Two transition probability matrices of a stage-structured life-cycle model of tansy ragwort. Matrix elements (SF = spring to fall transition; FS = fall to spring transition) represent the probabilities that individuals in one size class year t (columns) will enter a class year $t + 1$ (rows). Zero's indicate transitions that do not exist or were not calculated for this study. For values see Table A1.

	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	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 site's respective seed survival rate as found from the seed burial study explained in the text.

The five classes in the life-cycle model were represented in each projection matrix with five rows and five columns. Each arrow in the life-cycle model corresponds to a coefficient in the matrix. Since we mapped individuals at two different times of the year (spring and fall), we have two transition matrices (Table 4). The matrix elements SF (spring-to-fall) and FS (fall-to-spring) define transitions from stage j to stage i . The fate transitions are a proportion and vary between 0 and 1, whereas the fecundity transitions are an integer, and can have values higher than 1. A basic matrix model can describe the population dynamics of plants in which the fecundity and mortality schedules have been calculated in relation to life state (Caswell 1989). Depending on the monitoring time interval, it is possible for an individual to remain in a particular stage category, move up at least one stage, or even revert to an earlier life-stage.

The dominant eigenvalue of the projection matrix is equivalent to the finite rate of increase, λ , of the population at stable stage distribution. However, with two transition matrices per generation, we measured λ at the generation where it became stable for all environments (20 generations).

The experiment was started in spring 2001, which allowed the construction of two spring to fall matrices per study site, one for 2001 and one for 2002, and one fall to spring matrix per study site, for 2001-2002. Initial population was found to not affect λ distributions. Therefore, the initial population vectors were represented by fall 2001 mean values of seeds, seedlings, rosettes, flowering plants, seed produced, and seed bank found in each environment. The simulation model runs by first multiplying the fall to spring transition matrix by the initial fall population vector to yield the spring population.

Then the spring population vector is multiplied by the spring to fall transition matrix to yield the projected fall population. It was from the projected fall population of rosettes plus flowering plants (N) that λ was calculated ($\lambda = N_{t+1} / N_t$, where N is the population size).

Model Simulations

To accomplish objective 4, Monte Carlo simulations were used to evaluate how the different environments affected tansy ragwort population viability and potential invasiveness. Since transition parameter values were calculated for each plot (subsample) in each environment and for each transition period (spring to fall and fall to spring), a set of transition values from a plot was selected and used to simulate the population dynamics (growth) for 20 years (generations). This process was repeated 1000 times, with a different plot randomly selected for each simulation to accumulate a distribution of λ values for each environment type.

Elasticity Analysis

In order to accomplish objective 5, to identify transitions (demographic processes) that are proportionally most important in regulating tansy ragwort population size, perturbation/elasticity analysis was performed. Specifically, elasticity analysis was used to investigate how population size (density) changes when mean transition parameter values were individually perturbed. Elasticity was defined in this study as the proportional change in density of rosettes plus flowering plants in the fall (N_{t+10}), caused by a proportional (10% reduction) perturbation to transition matrix parameter values.

Elasticity values reflect the relative impact of each transition matrix parameter on population growth rate (Caswell 1989). Elasticity values for this study were reported as values ranging from 0 to 100, where 100 had the greatest impact on population density. Elasticity analysis can identify vulnerable life history stages of tansy ragwort associated with specific demographic processes.

Environmental Variables

To quantify the relationship between specific environmental variables including soil characteristics and the most important transitions as found with elasticity analysis (Objective 6), I used linear regression. Soil samples were collected from eight of the ten study sites in late May 2002. Mineral soil to a depth of 10 cm was collected adjacent to each of the 1 m² demographic plots, for a total of 85 soil samples. Soil was dried at 49 °C for 48 h, then ground by hand using a pestle and mortar and sieved to remove coarse fragments. Total N, organic matter, pH, particle size, and major nutrients (P, K, Mg, and Ca) were analyzed by MDS Pharma Services, Inc. (in Lincoln, Nebraska). Percent cover of other plant species and abiotic features (i.e., rocks, downed woody debris, and bare soil) were recorded for randomly selected 1m² plots at each of the ten study sites.

Statistical Analysis

Statistical analyses were performed with SAS 9.0, Minitab 13.1, S-Plus 2000, and Excel XP. To calculate transition rates (Objective 1), differences between seed viability data obtained from the seed burial experiment were analyzed in SAS 9.0. The response variable, viability, can be considered as a binomially distributed response, thus it was

transformed to the logit scale. The transformed data was tested for normality by plotting the residuals. The residuals fit a straight line, indicating that the data fit normal quantiles. Also, the Shapiro-Wilk (SAS 9.0 2003) coefficient was 0.91 ($P < W = 0.0647$), indicating normality in the transformed data. The data also met the assumption of homogeneous variance as tested by plotting the predicted values against the residuals. Because these assumptions were met, the generalized linear mixed models procedure was appropriate to test for main treatment effects (environments). The null hypothesis was that percent seed viability was equivalent within the four environments evaluated after a ten month burial treatment.

The median transition rates for the four different environments (Objective 2) were qualitatively compared using box and whisker plots that included 95% confidence intervals for the medians. If median confidence intervals for two boxes did not overlap, I considered the two medians to be different at an approximate 5% significance level (S-Plus 2000). The median was chosen as the measure of central tendency for the above analyses due to the skewed distributions of the transition parameter data. The null hypothesis was that median transition rates were not different among the four environments.

Objective 3, testing for density dependence, was accomplished using simple linear regression. The null hypothesis was that neither intra-specific nor inter-specific density dependence influences the demographic processes of tansy ragwort populations sampled in the Kootenai National Forest.

Objective 4 was accomplished by comparing population growth rates (λ) for each environment. Confidence intervals for median λ s were displayed using box and whisker plots. The probability of difference in λ between environment types was calculated by conducting Monte Carlo simulation where plot-specific transition parameters were selected at random 1000 times for each environment and then summing the number of times that λ for one environment was greater than λ for another environment and dividing by 1000. In addition, the probability of $\lambda > 1.0$ (defined as locally invasive) was given for each environment by calculating the proportion of simulation iterations resulting in a λ greater than 1.0. The magnitude of λ signifies whether a population described by the matrix is locally invasive ($\lambda > 1.0$), stable ($\lambda = 1.0$), or locally decreasing ($\lambda < 1.0$). All model calculations were performed in Excel XP with programs and population analysis macros programmed by Bruce Maxwell (Appendix D).

Three different Monte Carlo simulations were run using different values for the seedling to rosette transition (emergence rate probabilities) and different fecundity values. The population growth rates resulting from the three simulations were compared using the probability of $\lambda > 1.0$ for each simulation approach. The null hypothesis was that λ did not differ among environments.

Objective 5 was accomplished by calculating elasticity values for each transition parameter using mean transitions for each environment. Mean transitions were used for this analysis instead of median values in order to account for extreme values. Objective 6 was accomplished by quantifying the relationship between soil characteristics and the two transitions found to be most important with elasticity analysis using Pearson's

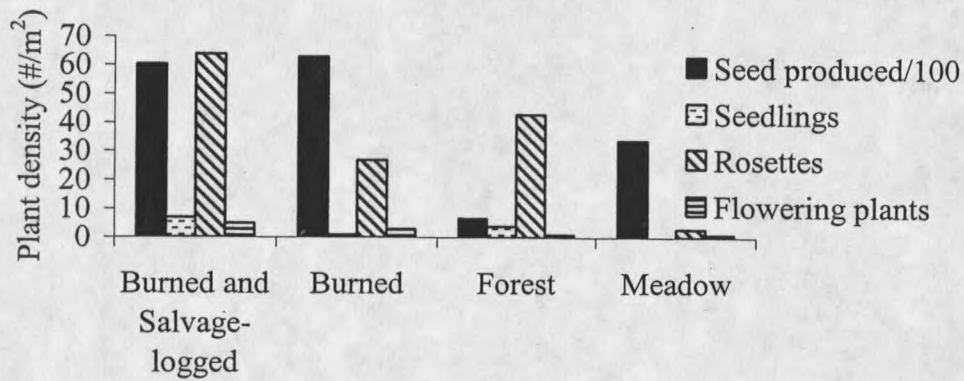
correlation. Regression analysis was run to further examine the relationship for environmental variables having a correlation value greater than 0.5 and/or p-values less than 0.05. The null hypothesis was that there was no correlation between environmental variables (soil characteristics and vegetation cover) and important transition rates.

Results

Transition Rates

To quantify transition rates between tansy ragwort population life history states, individuals were censused in four different environments. In 2001, the Burned and Salvage-logged sites had the most rosettes and flowering plants of all four sites, followed by the Forest, then Burned, then Meadow sites (Figure 3, Table 5). The number of adult plants (rosettes plus flowering plants) per sample plot ranged from 1 to 183 in the first year of the experiment. The 2002 distribution of life-stages is similar to the 2001 distribution. However, in 2002 flowering was less frequent than in 2001. In 2001, there was only one individual flowering in the Forest and Meadow. The effect of the reduced flowering in 2002 will not be known until the 2003 data is collected. Tansy ragwort germinates in both fall and spring. A small number of seedlings were censused in the fall, but the majority of recruitment occurred in the spring.

A: Fall 2001



B: Fall 2002

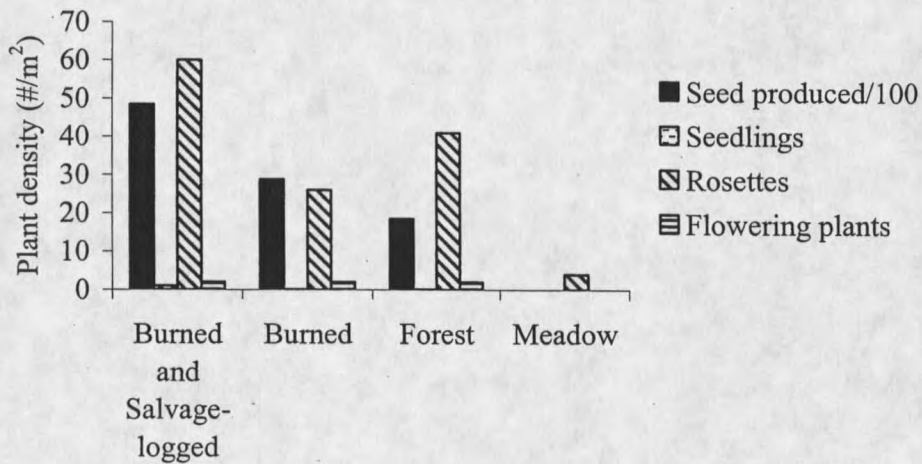


Figure 3. Mean density of tansy ragwort individuals in each life-history stage in four environments in fall 2001 (A) and fall 2002 (B). The life cycle was divided into five stages (see text for explanation). Seed produced values were divided by 100 so that all four stages could be represented in the same figure.

Table 5. Mean number of rosettes (and standard deviation) and flowering plants (and standard deviation) in four different environments.

Site	Fall 2001		Fall 2002	
	Rosettes	Flowering	Rosettes	Flowering
Burned and Salvage-logged	64 (48)	5 (6)	60 (46)	2 (3)
Burned	27 (26)	3 (3)	26 (26)	2 (2)
Forest	43 (36)	1 (1)	41 (35)	2 (1)
Meadow	3 (2)	1 (1)	4 (4)	0 (0)

Fewer seedlings, on average, established in spring 2002 than in spring 2001 in each of the environments except in the Meadow where an average of two seedlings was censused in spring 2002. In the Burned and Salvaged-logged sites, of the 116 new rosettes that were censused during the study in spring 2002, 10% were clonally produced daughter rosettes, emerging from the root or caudex of post-flowering individuals. Out of a total of 69 new rosettes that were counted in the Burned sites, 5% were clonally produced daughter rosettes while the rest originated from seedlings. Three new rosettes and one new rosette were found in the Forest and Meadow, respectively, and none were clonally produced. Ten percent of the population in the Burned and Salvaged-logged sites and 5% in the Burned sites had an iteroparous (reproducing more than once) life cycle.

Seedling Emergence Experiment

The seedling emergence rate was 25% in early spring 2001 in the Burned and Salvaged-logged environment, 15% in the Burned, and no seedlings emerged at either the undisturbed Forest or Meadow environments. No seedlings were observed at any of the four environments one year later in 2002.

Seed Bank

The seed used in the seed burial experiment was 82% viable before burial. Seed retained in a dark laboratory drawer was 75% viable after ten months. Seed buried for ten months in the Forest and the Meadow soils had the highest mean percent viability (Table 6). Seed buried at the burned sites had the lowest mean percent viability after ten months. Based upon differences of least squares means, there were no differences in seed viability after 10 months of burial among the environments, except between the burned environments and the Meadow environment ($t = -2.34$, d.f. = 9, $P > 0.0441$) and between the burned environments and the seed viability before burial ($t = -2.40$, d.f. = 9, $P > 0.04$) (Figure 4).

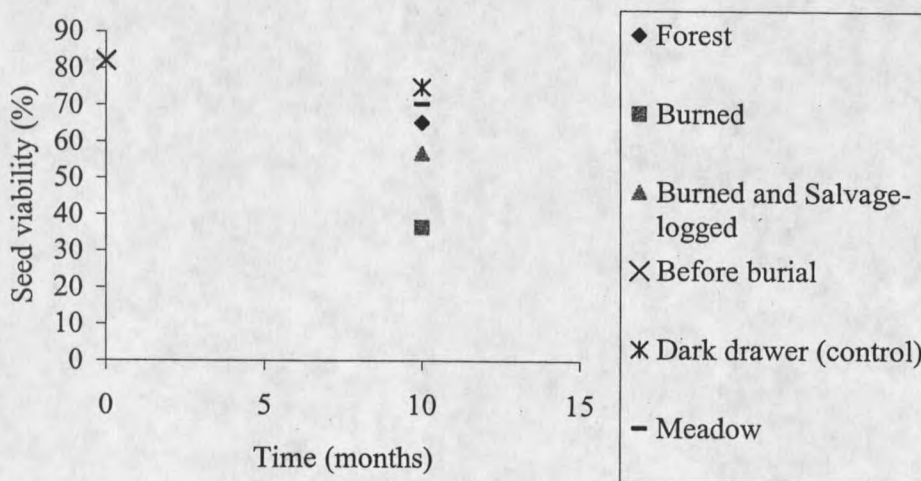


Figure 4. Mean seed survival by environment. Burned and salvage-logged ($n = 8$); Burned ($n = 8$); Forest ($n = 2$); Meadow ($n = 2$).

Table 6. Mean percentage viability over time (and standard deviation) of stored seed and of seed buried at 2 cm in four different environments.

Time (months)	Mean viable seed				
	Stored (%)	Burned and Salvage- logged (%)	Burned (%)	Forest (%)	Meadow (%)
0	82	82	82	82	82
10	75	57 (19.3)	37 (19.5)*	65 (8.9)	70 (9.5)*

*Comparisons significant at $\alpha = 0.05$.

Seed buried in the Burned environments lost viability more rapidly than seed buried in the other three environments. Seed buried in the two undisturbed sites (Forest and Meadow) lost viability much more slowly than the two burned sites, but not as slowly as the dried laboratory-stored seed. If the seed decay rate or loss of viability was assumed to be constant in each environment the years to reach low viability (1%) could be calculated. The Burned environment was forecasted to take only 5 years to 1.0% viability, whereas the Forest environment was forecasted to take seeds 23 years to reach low (1.0%) viability (Table 7).

Table 7. Predicted time (years) to reach 1% viability in the soil. Annual decrement in viability is assumed to be constant with time.

Soil depth (cm)	Years to 1% viability				
	Air storage	Burned and Salvage- logged	Burned	Forest	Meadow
2	41	10	5	23	16

Comparing Mean and Median Transition Rates

Mean transition values were calculated from the transition rates quantified in 2001 and 2002 for each of the four environments (Table 8).

Table 8. Mean transition values for field plots from four environments.

Sites ^b	Mean transition values ^a										
	SF1	SF2	SF3	SF4	SF5	FS1	FS2	FS3	FS4	FS5	FS6
BSL n=40	0.731	0.844	0.093	0.005	0.579	1134	0.775	0.053	0.276	0.033	0.623
B n=40	0.588	0.739	0.162	0.001	0.450	1162	0.790	0.042	0.175	0.022	0.497
F n=10	0.870	0.879	0.053	0.003	0.717	851	0.873	0.000	0.575	0.021	0.706
M n=5	0.275	0.755	0.128	0.000	0.649	1352	0.871	0.000	0.000	0.001	0.649

^a see Figure 2 for definition of transition rates

^b BSL = Burned and Salvaged-logged, B = Burned, F = Forest, M = Meadow; n = number of plots (1 m²) used to calculate mean

Comparing the transition rates between years and environments showed that demographic parameters for tansy ragwort did not vary in distribution from 2001 to 2002 with the exception of the seedling to rosette transition (SF1) from spring to fall. This parameter was, on average, lower in 2002 and much more variable than in 2001 (Figure 5). Demographic parameters varied by environment, in distribution (e.g. Figure 5), in shape of distribution (non-normal) and in central tendency (median). Thus, box and whisker plots were used to qualitatively assess differences between environments, allowing for the true distribution and central tendency to be visualized.

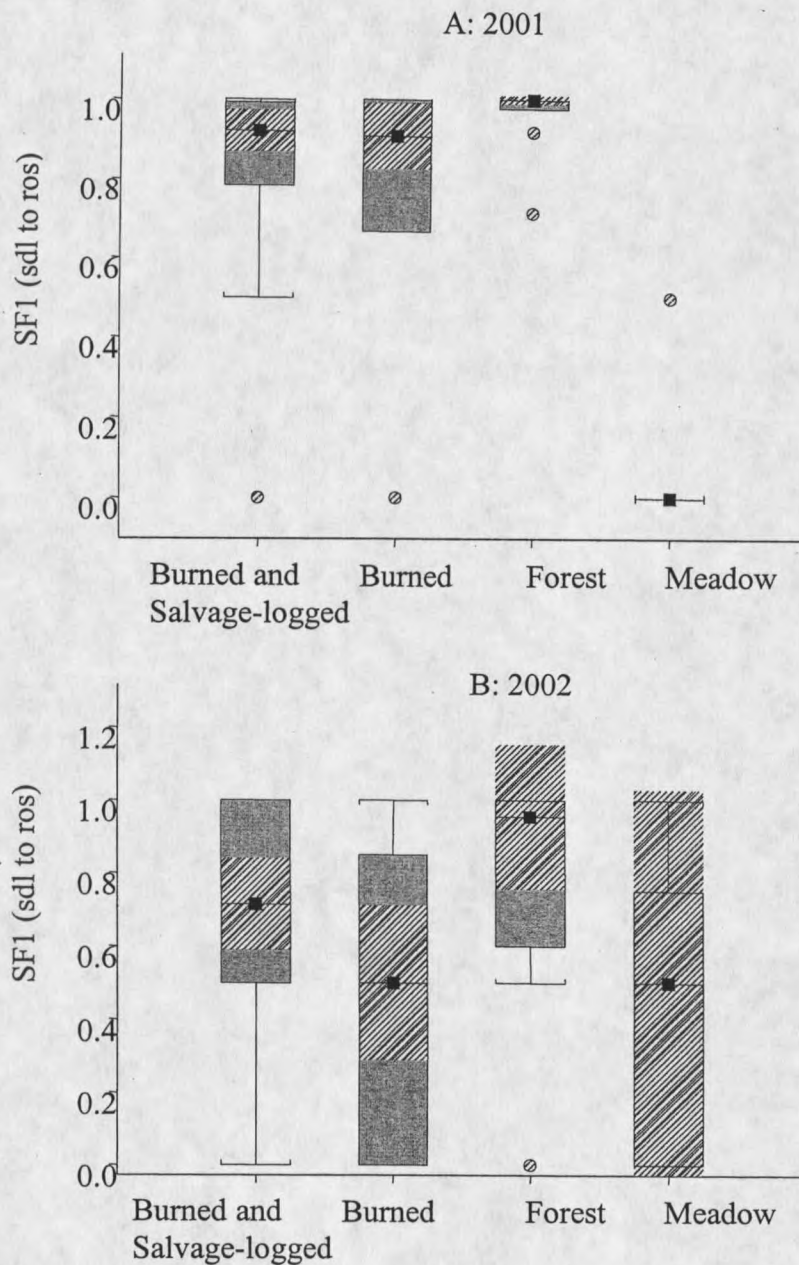


Figure 5. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments. See Appendix A for more figures comparing median transition rates for the four environments.

All parameters representing a progression up from one life-history stage to the next (rather than remaining in the same stage or reverting to an earlier stage) were greater in 2001 than 2002 for the spring to fall transitions. Only one fall to spring census was performed during this study, thus only one set of fall to spring transition matrices were available. All of the fall to spring transitions were similar regardless of environment, with the exception of the seedling to rosette transition (FS4), which differed significantly between the Burned and Salvage-logged sites and the Forest sites (i.e. the 95% confidence intervals for medians did not overlap).

Fecundity values (FS1) varied by environment. In 2001, the flowering plants in the Burned and Salvage-logged sites produced the most seed, whereas in 2002, the most seed was produced by Forest tansy ragwort plants. Fecundity (FS1) is the number of seed produced per plant.

The least variable transition parameter was the rosette to rosette transition, both from the spring to fall and from the fall to spring (SF2 and FS2). This parameter estimate was also consistently higher than other survival transitions.

Population Growth Rates

Under unchanging conditions, λ (the equilibrium finite rate of increase) is a measure of population viability (Caswell 1989). Simulations of population growth in the Burned and Salvage-logged environments with 1000 replications of randomly selected plot transition values produced a calculated mean λ of 1.369, indicating population growth. The mean λ for the Burned environments (1.226) also suggests population growth under conditions observed during the study period. The Forest population growth

rate ($\lambda = 1.064$) indicated a nearly stable population size if conditions were to remain constant. Populations would probably decline in the Meadow environment ($\lambda = 0.788$) under 2001 and 2002 measured transitions.

Individual tansy ragwort populations varied in λ s calculated from simulations across environments (Figure 6). Based on mean and median λ s, two of the four populations were invasive ($\lambda > 1.0$), one was nearly stable ($\lambda = 1.0$), and one was declining ($\lambda < 1.0$). Thus, based on two years of data, the two populations in disturbed environments will increase, while the two undisturbed populations will remain fairly stable or decrease if conditions during the study remain constant.

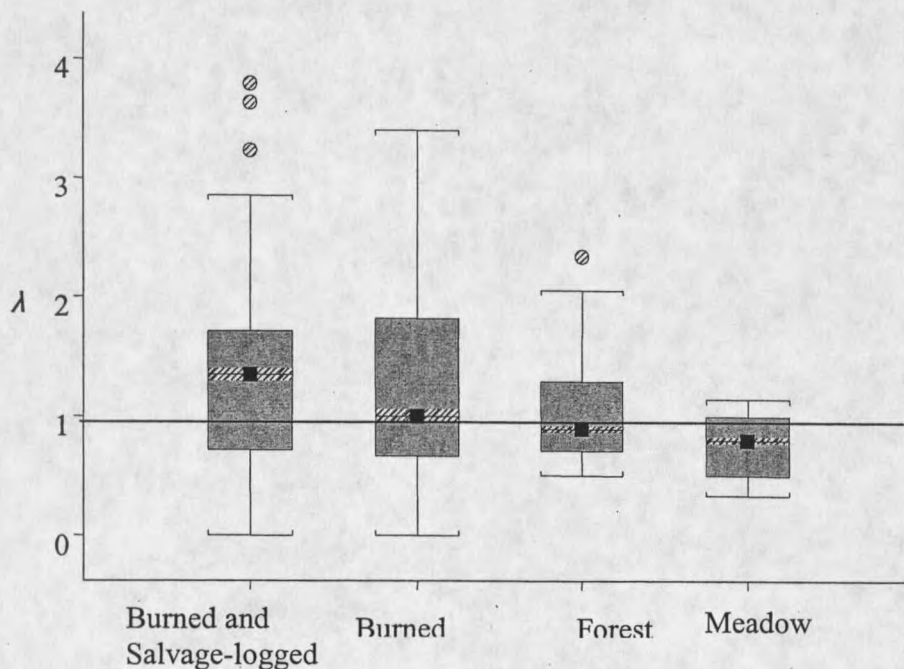


Figure 6. Median population growth rates (λ) of tansy ragwort. Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments. If the confidence intervals for two boxes do not overlap, this indicates a difference in location at an approximate 5% significance level.

The 95% confidence intervals for the median λ s do not overlap for any of the four environments, indicating a significant difference ($\alpha = 0.05$) (Figure 6). However, considerable variation in λ values occurs between plots (reps) within the same environment, especially within the Burned and Salvage-logged sites (CV = 60.0%) and the Burned sites (CV = 67.2%). Thus, to more rigorously assess population growth differences between environments, the 1000 simulated λ s (one from each environment) were drawn at random, 1000 times. The number of times that λ_i is larger than λ_j divided by 1000 is the probability that λ_i was greater than λ_j where i and j are different environments (Table 9). The highest probability of difference occurred between the Burned and Salvage-logged environment and the Meadow environment ($P = 0.671$) (Table 9). Another way of stating these results would be to say that only 30% of the Meadow tansy ragwort populations would have growth rates higher than populations found in Burned and Salvage-logged environments.

Table 9. Probability that top row environment λ will be greater than left-column environment λ .

Environment	Burned and Salvage-logged	Burned	Forest	Meadow
Burned and Salvage-logged	-	0.46	0.38	0.29
Burned	0.54	-	0.47	0.37
Forest	0.62	0.53	-	0.37
Meadow	0.71	0.63	0.63	-

Model Simulations

The parameterization of the tansy ragwort model had two potential weaknesses that could alter conclusions drawn with model simulations: 1) The emergence rates

needed to be more fully assessed. Understanding the factors that regulate emergence may be especially important for predicting the occurrence of new colonies. 2) Fecundity values were not collected on all plots. 3) Only one or two years of data were used to estimate transition parameter values. The mean, median, and modal length of a PVA is about four years. Debate continues over whether such short periods of study can result in PVAs that truly represent a species' population dynamics (Menges 2000).

In the initial simulations described previously (Figure 6), emergence rates were calculated based upon censused new seedlings as a proportion of seed produced per plot the previous fall multiplied by the mean survival rate for each respective environment. This calculation yielded emergence probabilities in concurrence with values reported from previous studies (from <1 to 10% per plot) (Meijden and Waals-Kooi 1979), but I have low certainty about those values because I do not know exactly how many seed were in the soil and actually germinated and emerged as seedlings. The seed produced per plot values used in the emergence calculation were estimates, not exact values.

The seed sowing experiment yielded an emergence rate for the Burned and Salvage-logged and the Burned sites, but no seedlings emerged in the undisturbed Forest and Meadow seed sowing experiments. There must be some low probability of emergence in order for populations to exist in these environments. To test the sensitivity of the emergence rate parameter, I performed a second simulation using the seed sowing experiment values for the spring to fall matrix. I assumed an emergence rate of 0.001 for both the Forest and Meadow based on low values reported in the literature (Meijden and Waals-Kooi 1979).

Using the emergence rates from the field seed sowing experiment in the spring to fall matrix yielded higher mean λ values for all of the environments except the Meadow (Table 10). The distribution of λ s was the same as found in the first simulation, and hence the probability of λ being different between environments was similar. However, coefficients of variation were higher for the two burned sites for the second simulation (Simulation 2).

Table 10. Mean population growth rates (λ) (and standard deviation) in four environments for three different simulations of the tansy ragwort model.

	Simulation 1 ^a			Simulation 2 ^b			Simulation 3 ^c		
	λ	Prob. $\lambda > 1.0$	CV (%)	λ	Prob. $\lambda > 1.0$	CV (%)	λ	Prob. $\lambda > 1.0$	CV (%)
Burned and Salvage- logged	1.369 (0.822)	0.548	60	1.649 (1.166)	0.572	70.7	1.158 (0.61)	0.502	52.7
Burned	1.226 (0.824)	0.468	67.2	1.339 (1.125)	0.449	84	1.061 (0.63)	0.447	59.4
Forest	1.064 (0.526)	0.407	49.4	1.067 (0.48)	0.418	45	1.01 (0.412)	0.333	40.8
Meadow	0.788 (0.27)	0.131	34.3	0.776 (0.267)	0.11	34.4	0.758 (0.25)	0.115	33

^a SF4 = $SDL_{fall,t+1}/(SP_{fall,t} * \text{mean survival rate})$; FS5 = $SDL_{spring,t+1}/(SP_{fall,t} * \text{mean survival rate})$

^b SF4 = for Burned and Salvage-logged = 0.25; for Burned = 0.15; for Forest and Meadow = 0.001; FS5 = same as Simulation 1

^c SF4 = same as Simulation 1; FS5 = same as Simulation 1; FS1 = seed produced per plant two times smaller than values for Simulations 1 and 2

Fecundity was defined as seed produced per plant and was extrapolated from randomly sampled flowering plants. While seed produced from flowering plants in the four environments was counted, the mean was often used for plots where flowers were not sampled, increasing the potential for inaccurate estimates of fecundity. The third

simulation (Simulation 3) included fecundity values that were 2 times smaller than the seed produced per plant values used in the first simulation. The resulting mean λ s for this alternative simulation have the same distribution as the original simulation; however, the standard deviations are lower for the two burned sites (Table 10).

Elasticity Analysis

To meet objective 5, I performed elasticity analyses for the average transition matrix values for each environment at three levels of percent change in parameter value: -10, -5, and -2.

Table 8 shows average transition values for each environment. Changing parameter values by 10% yielded the most consistent results over 5, 10, 20, and 40 generations. The overwintering period of the rosette (FS2) was of overwhelming importance in the life cycle of tansy ragwort in each of the four environments. Second in significance to the FS2 elasticity value was the survival of rosettes from the spring to the fall (SF2).

Changing parameter values by 5% yielded fairly consistent results, with the highest elasticity value associated with overwintering rosettes (FS2). However, changing parameter values by 5% over only 5 generations yielded a shift in important parameters within the two burned sites (Table 11). I chose to analyze elasticity over just 5 generations in order to capture a possible exponential phase of population growth that would be typical after initial invasion of tansy ragwort to a new environment. Over just 5 generations, the most important transitions in the Burned and Salvage-logged and the

Burned sites are the seed bank to seedling transition from fall to spring (FS5) and the seedling to rosette transition from spring to fall (SF1).

Table 11. Elasticity values (0-100) using mean transition rates (Table 8) for each environment with a -5% change in parameter values over 5 generations. Values of 100 are most important.

Transition	Burned and Salvage-logged	Burned	Forest	Meadow
FS5 (sb to sdl)	92.635	100	0.815	0.604
FS4 (sdl to ros)	3.222	0.538	0.489	0
FS2 (ros to ros)	100	36.694	100	100
FS3 (flw to ros)	0.304	0.358	0	0
FS1 (flw to spp)	7.098	11.919	3.608	0.402
FS6 (sb to sb)	9.874	8.614	0.122	0.413
SF4 (sb to sdl)	2.824	0.47	0.312	0
SF1 (sdl to ros)	92.635	100	0.815	0.604
SF2 (ros to ros)	35.205	9.524	74.057	80.453
SF3 (ros to flw)	45.258	33.996	4.174	0.305
SF5 (sb to sb)	9.977	8.506	0.22	0.413

Changing parameter values by 2% resulted in the least consistent elasticity values across environments. At 40 generations, the survival and growth parameters all had elasticity values in the 90's. At 20 generations, 3 of the 4 environments had elasticity values of 100 for the rosette to flowering transition from spring to fall, with the exception being the Forest. At 10 generations, the emergence of seedlings from fall to spring (FS5) was most important in the two burned sites, while the survival of rosettes (SF2) was most important in the Forest; and in the Meadow emergence of seedlings in the spring (FS5) was most important. At just 5 generations with a 2% change in parameter values, the rosette to flowering transition from spring to fall (SF3) was most important in the two burned sites, whereas in the Forest, fecundity (FS1) was most important, and in the Meadow, overwintering rosette survival (FS2) was most important.

Elasticity values calculated at 20 and 40 generations indicated for the average transition matrix that the same transitions were important across environments and were associated with the rosettes (Table 12). The overwintering of rosettes appeared to be proportionally the most important transition regulating tansy ragwort population size, followed by the survival of rosettes from the spring to the fall.

Table 12. Elasticity values (0-100) using mean transition rates (Table 8) for each environment with a -10% change in parameter values over 20 generations. Values of 100 are most important.

Transition	Burned and Salvage-logged	Burned	Forest	Meadow
FS5 (sb to sdl)	0	0	0	0
FS4 (sdl to ros)	0	0	0	0
FS2 (ros to ros)	100	100	100	100
FS3 (flw to ros)	0	0	0	0
FS1 (flw to spp)	0	0	0	0
FS6 (sb to sb)	0	0	0.001	0
SF4 (sb to sdl)	0	0	0	0
SF1 (sdl to ros)	0	0	0	0
SF2 (ros to ros)	22.167	11.389	70.236	82.217
SF3 (ros to flw)	0	0	0	0
SF5 (sb to sb)	0	0	0	0

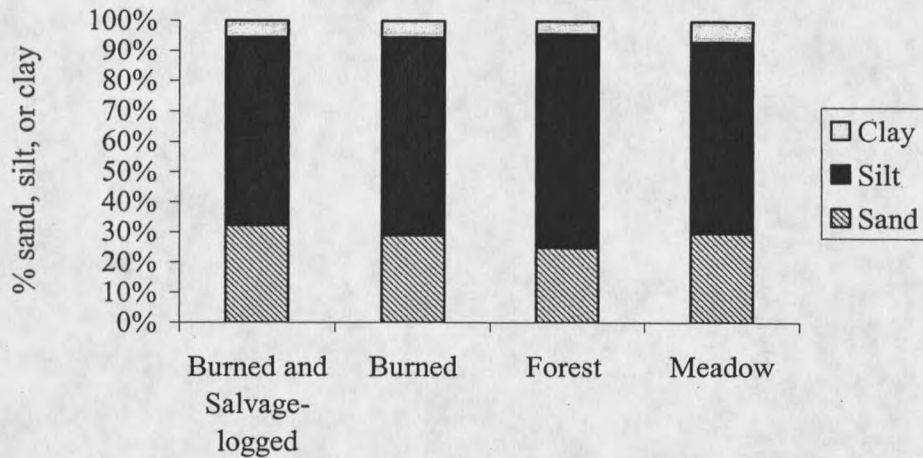
Environmental Variables

In consideration of objective 6, I quantified the relationship between specific environmental variables, including soil characteristics (Table 13), vegetation cover, and mean transition rates found to be most important in the elasticity analysis (FS2 and SF2). Each of the sampled plots had similar amounts of percent sand, silt, and clay and similar amounts of CEC species (Figure 7).

Table 13. Selected chemical properties and mean vegetation cover of burned and salvage-logged (n = 40), burned (n = 30), undisturbed forest (n = 10), and undisturbed meadow plots (n = 5).

Environment	CEC	pH	Total N (g/kg)	OM (%)	Mean Vegetation Cover (%)
Burned and					
Salvage-logged	12.33	6.5	0.21	5.23	14.3
Burned and					
Salvage-logged	7.39	6.3	0.10	2.48	33.5
Burned and					
Salvage-logged	12.13	6.2	0.17	6.79	31.3
Burned and					
Salvage-logged	10.79	6.1	0.14	3.62	27.4
Burned	8.13	6.4	0.09	3.06	42
Burned	14.03	5.8	0.22	9.86	47.4
Burned	9.88	6.4	0.14	3.23	19.2
Forest	7.66	5.9	0.18	2.79	27.7
Meadow	11.72	5.6	0.24	7.92	72

A: Soil texture



B: CEC species

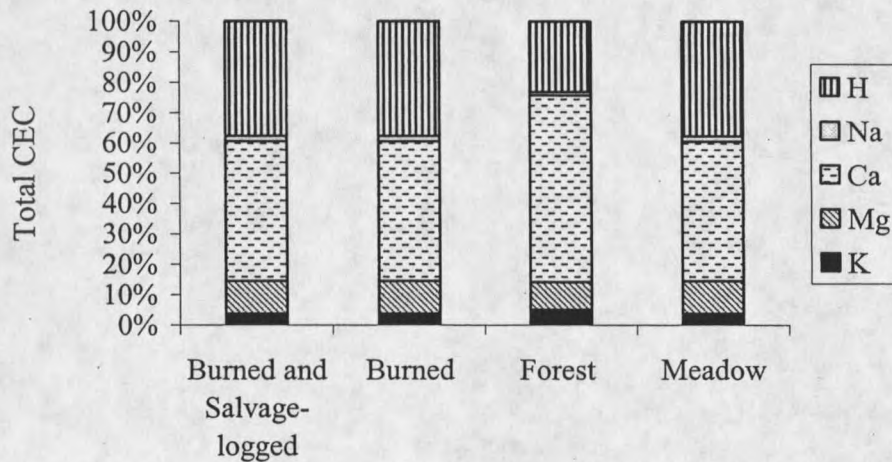


Figure 7. Mean percent sand, silt, and clay (A) and mean CEC species (B) by environment.

Pearson's correlation matrix (Appendix C) results showed that a significant negative relationship existed in the Meadow environment between the amount of calcium

in the soil and the rosette to rosette transition (rosette survival) over winter (FS2) (Pearson correlation = -0.897, $P = 0.039$, $n = 5$) (Figure 8). A significant relationship also occurred in the Meadow between cation exchange capacity (CEC) and over winter rosette survival (FS2) (Pearson correlation = -0.961, $P = 0.009$, $n = 5$) (Figure 9). The relationship between percentage organic matter in the soil and over winter rosette survival (FS2) was significant (Pearson correlation = -0.947, $P = 0.015$, $n = 5$) (Figure 10). No significant relationships existed between any other soil characteristic and over winter rosette survival in any of the other environments, nor did significant relationships exist between spring to fall rosette survival (SF2) and soil characteristics.

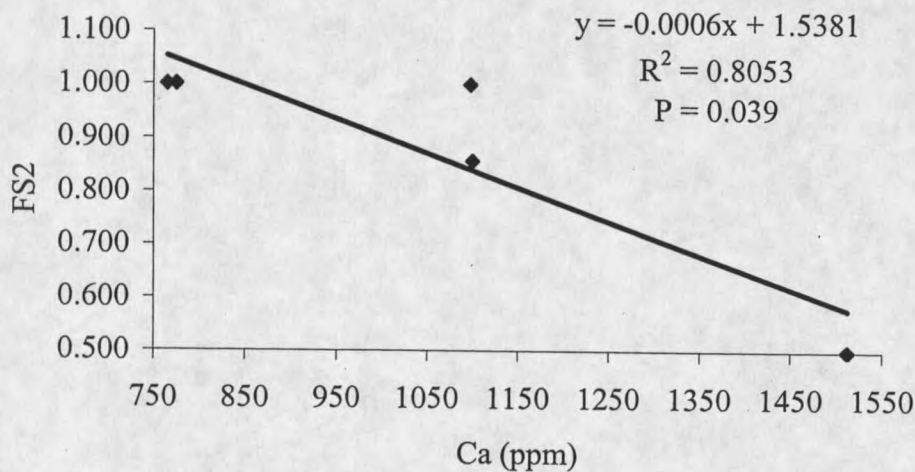


Figure 8. Relationship between the amount of calcium in the soil and the rosette to rosette transition over winter (FS2) in the Meadow environment ($n=5$).

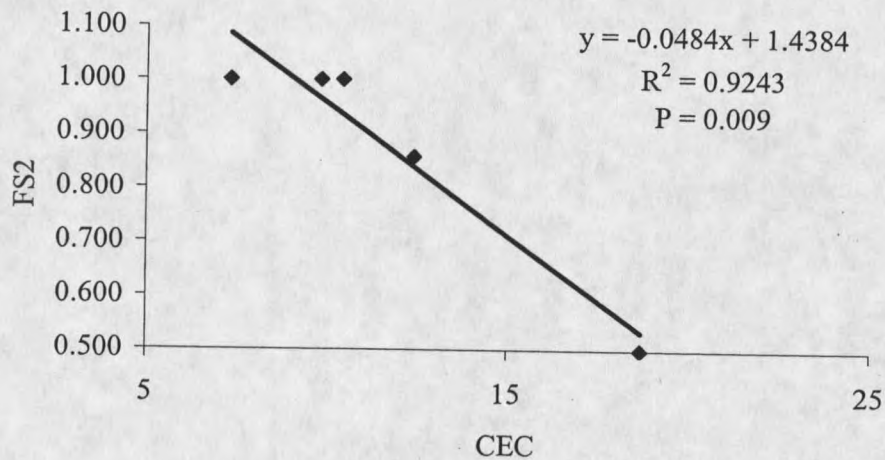


Figure 9. Relationship between the cation exchange capacity (CEC) in the soil and the rosette to rosette transition over winter (FS2) in the Meadow environment (n=5).

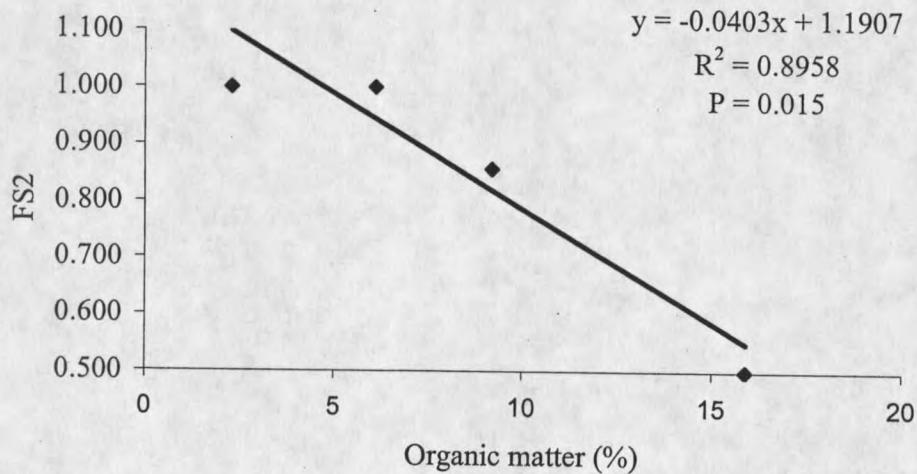


Figure 10. Relationship between percentage organic matter in the soil and the rosette to rosette transition over winter (FS2) in the Meadow environment (n=5).

No significant relationships were detected between percent cover of other plant species and the rosette to rosette transitions (FS2 and SF2) when tested for each

environment. A significant relationship was found between percent cover of other species and population growth rate (λ) in the Burned and Salvage-logged environments (Pearson correlation = -0.425, $P < 0.001$, $n = 40$) (Figure 11).

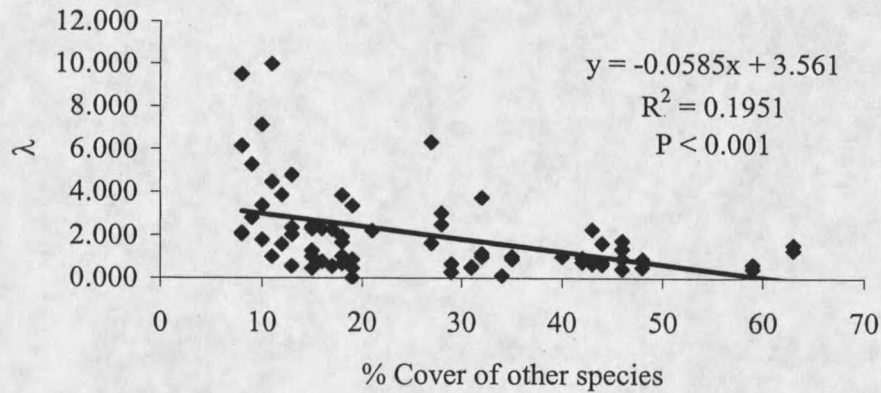


Figure 11. Relationship between percent cover of other species in plots and population growth rate (λ) in each plot in the Burned and Salvage-logged environment ($n = 40$).

Although no significant relationships were detected between percent cover of other species and λ in each of the other three environments separately, a linear regression of the data combined from all four environments yielded a significant regression ($P = 0.001$, $n = 95$). The Meadow had consistently low values of λ and higher percent cover of other species compared to the other environments (Figure 12).

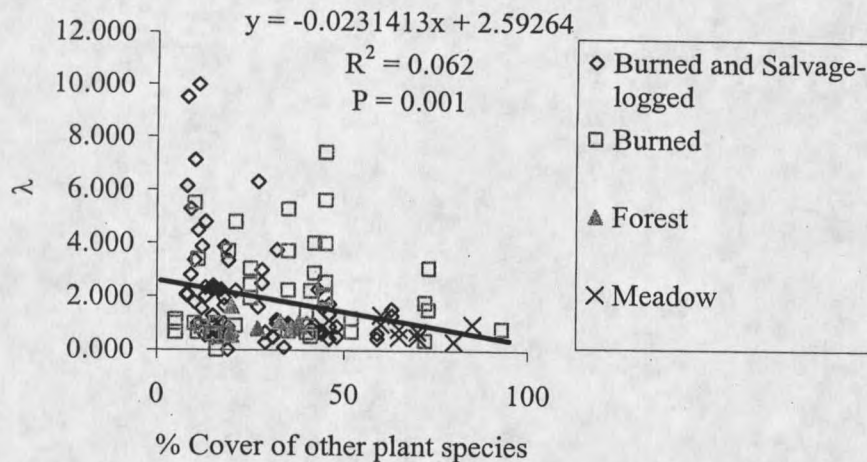


Figure 12. Percent cover of other species versus population growth rate (λ) of all populations sampled in each environment for 2001 and 2002 ($n = 95$).

Discussion

Modeling Population Viability

Based upon the results of my analysis after two years of data collection, tansy ragwort populations were locally increasing (invasive) in the Burned and Salvage-logged and the Burned environments. The first two years of this study indicated that disturbance had an effect on population viability of the invasive weed tansy ragwort. In particular, populations in the Burned and Salvage-logged environments and Burned environments had higher population growth rates than populations in the undisturbed Meadow. Higher transition rates, including the seedling to rosette transition from spring to fall and the flowering to seed produced per plant transition, in the two disturbed environments accounted for the differences. The sampled populations in the undisturbed Forest were not consistently decreasing or increasing ($\lambda = 1.0$).

Based on elasticity values, the survival of rosettes over winter contributes most to population growth of tansy ragwort in the four different environments. This finding is similar to results from previous studies on the effects of plant size and vernalization on the probability of over winter survival of tansy ragwort rosettes. Prins et al. (1990) showed that tansy ragwort plant size just before or just after winter is the primary determinant of flowering. The threshold rosette diameter was 10 cm. The Prins et al. (1990) study is relevant to the present study, because it reiterates the importance of the survival of rosettes over winter to tansy ragwort population growth.

In this study, significant relationships between soil characteristics and rosette survival over winter were detected only in the Meadow environment. This may be because the Meadow is a more homogeneous environment than the other three environments sampled in this study (i.e., the CV for the meadow tansy ragwort population growth rate was 33% versus 60% and 67% in the Burned and Salvage-logged and Burned environments, respectively). The meadow has a more continuous and intact cover of grass, whereas the two burned environments have a more disturbed soil surface layer and either less or more patchy vegetation cover, making those environments more spatially variable. All three significant relationships in the Meadow were negative relationships, meaning the higher the soil characteristic (calcium, CEC, and organic matter), the lower the rosette transition rate over winter. A possible explanation may be that in the Meadow environment where calcium, CEC, and organic matter are high, the density of other plant species is higher; hence, plant competition is more intense and tansy ragwort is less able to establish itself in such an area. The Meadow has not been

disturbed by wildfire or logging like the two burned environments, therefore fewer microsites exist in which tansy ragwort can germinate and become established. Also, calcium, CEC, and organic matter were all correlated with each other (see Appendix C), indicating that these three characteristics are related. The relationships between soil properties and important transition parameters explored with regression analysis must be interpreted with caution and further explored with controlled experiments to verify the existence of any true causative relationships.

In the Burned and Salvage-logged environments, population growth rates (λ) were lower where percent cover of plant species other than tansy ragwort was higher. Furthermore, combining data from all populations sampled in all four environments showed a significant relationship between λ and percent cover of plant species other than tansy ragwort, indicating that inter-specific density dependence is a factor in the population growth rate of tansy ragwort (Figure 12). For example, the Meadow had consistently low tansy ragwort population growth rates and higher percent cover of other plant species. The data scatter does seem to indicate a linearly decreasing upper limit to λ as other vegetation cover increased. Although the regression analysis indicates that only 6% of the variation could be accounted for, the p-value was quite low ($P = 0.001$). A noticeable cap exists on λ indicating a strong density response relationship. This supports findings from previous studies that favorable environments for individual tansy ragwort survival and growth have low, herb-dominated vegetation cover (Cameron 1935, Crawley and Nachapong 1985). Seedlings are particularly responsive to low cover (Crawley and Nachapong 1985).

Variation in λ values was high between populations within the same site type at the Burned sites and the Burned and Salvage-logged sites. The variation of λ among populations may be due to environmental conditions, genetic variability, phenotypic variability, or chance events. Although plots were established in four separate sites that were all burned and four separate sites that were all burned and salvage-logged, site-specific variation in biotic and abiotic factors may be high enough within environments to influence the population growth rate of tansy ragwort (see outliers, Figure 6). Factors influencing the growth of tansy ragwort in these sites may include burn intensity, canopy cover, abundance of other plant species, and topographic position (i.e., depressions/areas that collect or retain moisture more readily than others).

Canopy cover may also be related to the longevity (change in percent viability over time) of seed buried at 2 cm in the soil. In the burned environments, fewer plants existed, thereby reducing transpiration, and leaving more water available for tansy ragwort seeds to imbibe. These conditions result in higher seed death than in the undisturbed environments where plant cover was higher and moisture was therefore less available. Toole and Toole (1953) demonstrated that conditions promoting partial imbibition of seed are particularly unfavorable and result in early seed death. These unfavorable conditions for seed are likely to occur at or near the soil surface.

Furthermore, longevity estimates (time to reach 1% viability in the soil) indicate tansy ragwort may persist in northwestern Montana soils longer than seed tested in New Zealand by Thompson and Makepeace (1983). New Zealand estimates indicate that ragwort seed persists in the 0 – 2 cm depth layer at least 4 – 5 years and for at least 10 –

16 years when buried below 4 cm. The forecasted longevity for tansy ragwort seed buried in four different environments in northwestern Montana ranged from 5 years in the Burned sites to 23 years in the undisturbed Forest site assuming that the decay rate remains constant. A possible explanation for the slower decay rate and greater longevity of Montana seed may be lower humidity and precipitation relative to the North Island sites in the New Zealand study. Studies prior to the New Zealand experiment indicated that the longevity of tansy ragwort ranges between 3 and more than 22 years (Chippendale and Milton 1934, Institute 1977, Bedell et al. 1981), similar to the results from the present study.

Model Parameterization Problems

The tansy ragwort model seed bank survival rate was based on data collected after just one year of burial. While this is sufficient for modeling the effects of environment on tansy ragwort population dynamics over two growing seasons, the model output will be strengthened by the addition of survival rates calculated from older seed banks. Likewise, as the work described here is expanded to include more data from additional years, it will serve to fill-out the distribution of population growth rates over the range of environments. As more field-derived parameter values are included in the tansy ragwort model, more environmental variation will be captured, giving a more accurate characterization of the distribution of demographic parameters and subsequent population growth rate values.

The data collected thus far and described herein may not be adequate to quantify the relationships between environmental variables and transition parameter values.

Canopy cover could have been more accurately quantified with the aid of a fish-eye lens or densiometer, rather than the optical estimates made in 2001 and 2002. Density or plant volume, by species, as biomass surrogate variables to quantify background vegetation may also bolster the model and perhaps lend more insight into variables affecting tansy ragwort population growth. For example, McEvoy and Coombs (1999) found that background vegetation strongly reduced projected tansy ragwort population growth. They measured this effect by setting up a factorial experiment that involved clipped, removed, and unaltered treatments in the field (McEvoy et al. 1993). Setting up a factorial experiment in addition to continued mapping of individual tansy ragwort plants in northwestern Montana would be logistically difficult but may offer greater insights into factors regulating population growth.

A random sample of flowering plants was collected and every seed produced by those plants was counted. This method while precise for those sampled plants, is quite time-consuming and not an accurate way to extrapolate seed production by flowering plants not sampled. The more conventional method of estimating seed produced per plant, counting number of capitula, should be used for the duration of this study. Plans should also include continued sowing of tansy ragwort seed in controlled field plots to better quantify emergence rate from the seed bank in the four different environments. Some consideration should also be given to the adaptive significance of tansy ragwort's dimorphic achenes. The central disc achenes retain the pappus, have trichomes, and are lighter and more numerous than the peripheral ray achenes, which do not have a dispersal

structure at maturity. Also, McEvoy (1984b) found that under similar conditions (20 °C and 12 h light/dark), ray achenes were slower to germinate than disc achenes.

Possible Alternative Tansy Ragwort Models

The model was structured in such a way that it captured the salient aspects of the tansy ragwort life cycle without being too simple or too complex. To add more life stages or transitions to the model would increase the amount of time required for censusing individuals in the field. McEvoy and Coombs (1999) chose to structure their tansy ragwort model for populations on the Oregon Coast with only a few life history states and transitions. They pointed out that all individuals within a state could be treated as identical by the model, utilizing only a few life history states in the model reduces the accuracy of simulated dynamics but may still reveal general trends. On the other hand, models similar to the one discussed in this paper use more life history states, which in turn lead to a model with more parameters, allowing greater specificity in identifying processes to target for management of this weed. One concern about this approach is that it may make estimating parameter values difficult and cause inaccurate characterization, because sample sizes in each category are small.

Censusing twice during the growing season did add complexity to the modeling of tansy ragwort population dynamics in the Kootenai National Forest. Two censuses created a larger model including two transition matrices, doubling the number of demographic parameters. This was difficult because it was not always intuitive as to where certain parameters belonged within the two transition matrices. Having shown that the population growth rates of tansy ragwort vary among burned and salvage-logged,

burned, undisturbed forest, and undisturbed meadow sites, one can focus research on which environmental variables in those environments affects tansy ragwort population dynamics.

Implications for Management of National Forest Lands

After critically examining the assumptions underlying the tansy ragwort model, model projections can be assessed. Although model parameterization was limited to only two years of data collection, the findings indicate the necessity for management practices that limit disturbance of native vegetation cover to reduce seed germination and focus efforts on reducing survival of rosettes over winter.

The three different parameterizations and subsequent simulations with the model took into account a range of possible demographic parameter values and for those transitions where we had low confidence the model still produced similar probabilities of $\lambda > 1.0$ in each of the four environments. Thus, the model appears to be robust. Further, presenting the model results as probabilities of differences in growth rates based on Monte Carlo simulation utilizes the true distributions in the sample data. These probabilities help prioritize management of tansy ragwort infestations by ranking environments according to potential for population growth rates (λ) greater than 1.0 (invasiveness).

The first model simulation indicated that under conditions prevailing in 2001 and 2002, the growth rate of tansy ragwort populations were highest in the burned and salvage-logged sites (mean $\lambda = 1.369$; probability $\lambda > 1.0 = 0.548$), followed by the burned sites (mean $\lambda = 1.226$; prob. $\lambda > 1.0 = 0.468$). In these two environments, land

managers should focus on reducing adult survival as the most effective strategy to control the population growth of tansy ragwort. For example, any herbicide trials or monitoring of biological control agents should measure rosette survival as their primary dependent variable. Soil amendments with Ca or other ions to raise the CEC may be an effective way to reduce the spread of tansy ragwort if a causative relationship between CEC and critical transitions exists.

An elasticity analysis on a model of Oregon Coast populations of tansy ragwort with biennial or short-lived perennial life histories showed that fecundity was the major regulating transition for population growth in biennial populations compared with perennials (McEvoy and Coombs 1999). The elasticity analysis performed for the Montana study shows that rosette survival over winter is the most important for controlling tansy ragwort population dynamics. More accurate estimates of fecundity may show different results in Montana as this study is continued over the next few years. However, given the drier climate and the occurrence of earlier autumn frosts of northwestern Montana as compared to western Oregon, the present results make sense.

The Oregon site has warm and dry summers, cool and wet winters, with winter daily temperatures rarely falling below freezing. The mean annual rainfall is 252 cm, with 69% falling from November through March. The mean monthly temperature ranges from 5.1 °C in January to 15.7 °C in August (based on normals for the period 1951 – 1980). Comparatively, the mean annual minimum and maximum temperatures for the Montana site ranges from -3.09 °C to 12.51 °C. The mean annual precipitation is 56 cm (based on data since 1994). Previous studies have shown that tansy ragwort's capacity to

reproduce depends on environmental conditions of temperature and moisture and that this capacity decreases with summer drought and autumn frost (Harris et al. 1978, Cox and McEvoy 1983).

Conducting the tansy ragwort population viability analysis to include the construction of a life-history model was largely an exercise in accounting for competing influences within the system to the degree that their net effect could be estimated. The information gleaned from this study should help land managers make more informed and robust decisions. The forecasted population growth rates will help land managers prioritize specific environments to focus their efforts to reduce tansy ragwort population growth. The results of elasticity analysis identify specific demographic processes that should be targeted to effectively reduce tansy ragwort population size in northwestern Montana.

This study also illustrates that while tansy ragwort population growth rates in the Forest and Meadow environments may be lower than either of the burned environments, the longevity of seed in the soil seed banks of these environment types is much higher than in burned areas. Since burial below 1 cm and vegetation cover in the field inhibits immediate germination (Poole and Cairns 1940, Meijden and Waals-Kooi 1979, Thompson and Makepeace 1983) and dormancy may be induced by frost or drought, (Meijden and Waals-Kooi 1979) the relatively high seed viability in each environment after being buried for ten months indicate the necessity for management practices which limit seed burial to accelerate seed death.

The elasticity values and population growth rate differences between environments indicate that tansy ragwort populations are limited more by availability of microsites for germination and establishment than by availability of seed. McEvoy and Rudd (1993) found similar results in tansy ragwort populations on the coast of Oregon. Further, they found that the importance of microsites to tansy ragwort has notable implications for biological control. For example, although the cinnabar moth (*Tyria jacobaea* L.) larvae can strip the flowering shoot, removing all leaves and flowering heads and thereby reducing fecundity in tansy ragwort, regrowth often occurs; and as McEvoy and Rudd (1993) report, tansy ragwort abundance does not decrease even with significant levels of defoliation.

On the other hand, their study shows that the ragwort flea beetle (*Longitarsus jacobaea* Waterhouse) quickly reduced tansy ragwort survival, consequently decreasing local abundance. The flea beetle adults are pit feeders, rasping holes in the leaves of seedlings and rosettes. Flea beetle larvae tunnel and feed in leaves, petioles, stems, and roots during winter and early spring. Given its stage-specific host utilization patterns, the ragwort flea beetle may be an effective management tool for reducing northwest Montana populations of tansy ragwort.

This study's results on disturbance and colonization impacts on tansy ragwort population dynamics are consistent with earlier findings from seed-sowing (Cameron 1935, Crawley and Nachapong 1985) and disturbance experiments (McEvoy and Rudd 1993). These illustrate that the recruitment of seedlings varied among types of disturbance. Combining results of past experimental studies with the current field study

results establishes that disturbance is necessary in grasslands and forests to trigger ragwort recruitment from seed, regardless of whether the seed source is the seed rain or the seed bank.

Ecologists have emphasized how various types of disturbance are critical to the functioning of many natural communities and ecosystems (White 1979, Sousa 1984, Pickett and White 1985). Wildfire, for example, is an important natural disturbance in many ecosystems, especially dry coniferous forests of the U.S. Inland West (Arno 1980, Kauffman 1990). Ecologists frequently state that disturbed communities appear to contain many more weeds and alien species than undisturbed communities (Mooney et al. 1986, Oriens 1986, Hobbs 1989). In the case of wildfire, evidence supports the seemingly contradictory findings that many invasive nonnative species can be promoted and/or controlled by fire (D'Antonio 2000). Thus it is important to tease out the mechanisms that determine under what conditions an invasive species will be successful and using that information, influence considerations for managing invasive plant species, including the management of tansy ragwort in northwestern Montana.

Many forests in northwestern North America have evolved with wildfire and depend on that cyclical disturbance to maintain a succession of native species (Arno 1980, Kauffman 1990). However, with the introduction of non-indigenous plant species, land managers must be vigilant of invasive species that colonize disturbed areas following wildfire. Crawley (1986) has observed, that in his studies of the British flora, patterns of association have emerged, suggesting that invading plants are most likely to establish in communities where the average vegetation cover is low. Simberloff (1989);

Hobbs (1989) and others have denounced the lack of formal evidence, to support theories of invasion biology suggesting that disturbance is an important precursor to invasion, or that disruption of species interactions is the explanation for successful invasion. More work is needed for the development of theory that can predict the success or failure of invasions.

THE EFFECT OF SOIL SURFACE ENVIRONMENT ON TANSY RAGWORT EMERGENCE RATE

Introduction

Fire-induced changes on vegetation and soil characteristics have been studied for a long time. As non-native plant species are recognized as more of a problem in fire-prone plant communities, it is important that researchers identify the mechanisms that determine under what conditions an invasive species will be successful. Fire is both a natural and a human-induced disturbance that can either control or promote invasive species (D'Antonio 2000).

Tansy ragwort attained noxious weed status in Montana after populations were discovered in portions of the Flathead and Kootenai National Forests burned in a 1994 wildfire (Agriculture 2003). Isolated infestations have also been discovered outside the fire perimeter (Richardson 1997). Northern Rocky Mountain land managers suggest that the wildfires of 2000 and 2001 produced large tracts vulnerable to colonization by tansy ragwort. It is therefore important to link the temporal relationship between fire and invasion of tansy ragwort with environmental factors influencing this species successful colonization of the post-fire habitat. One way to accomplish this would be to explore the effects of soil surface environment on tansy ragwort germination and seedling emergence in burned and unburned environments.

This paper describes a greenhouse experiment conducted to specifically address the subject of tansy ragwort seedling emergence in response to created and selected

environments associated with fire. The goal of this experiment, repeated in the same year, was to determine the impact of the soil surface environment (litter, no litter, burned litter, heated bare soil) on tansy ragwort emergence rate. The null hypothesis tested was that soil surface environment has no effect on emergence and survival of tansy ragwort seedlings.

Previous disturbance studies with tansy ragwort show that growing vegetation and accumulation of litter can suppress germination in the field (Cameron 1935, Meijden and Waals-Kooi 1979, Crawley and Nachapong 1985, McEvoy and Rudd 1993). Other observations by land managers suggest that tansy ragwort seedling populations are common in burned forest areas, particularly in areas where slash had been piled and burned. Therefore the recruitment of individuals from the seed bank into a population of actively growing seedlings may depend on disturbance that removes vegetation and litter.

Although wildfire can promote invasive non-indigenous species, fire treatments are used to control many introduced species (D'Antonio 2000). These are important considerations in managing invasive plant species, notably tansy ragwort in northwestern Montana.

Periodic disturbance, such as wildfire in northwestern North America helps native plant communities maintain a succession of native species (Arno 1980, Kauffman 1990). With the introduction of non-native plant species, land managers must be vigilant in detecting invasive species that colonize areas disturbed by wildfire. Studies indicate that invading plants are most likely to establish in communities where the average vegetation cover is low (Crawley 1986). However, other ecologists have declared that more formal

evidence is needed in support of disturbance being a precursor to invasion (Hobbs 1989, Simberloff 1989). Clearly, more empirical evidence is required to test the theories that have been suggested in order to predict the success or failure of plant species invasions.

Early studies that experimented with tansy ragwort's response to fire did not produce conclusive evidence of the species responding favorably to fire-induced disturbance. Poole and Cairns (1940) experimented with using a flame thrower to control tansy ragwort, but their results were inconclusive and have not been reproduced by others. Mastroguiseppe et al. (1982) conducted several control burns at a tansy ragwort infested site in Redwood National Park, California, but those results were also inconclusive with regard to characterizing the response of this weed to fire.

Soil response to fire is largely a result of interactions between fuel consumption and soil characteristics that influence soil heating. Impacts on vegetation and site productivity are also related to soil heating. Heat flux describes the rate of heat flow that is delivered to the plant or a soil horizon. The duration of heat flow and the resultant temperatures directly affect the soil-vegetation complex (Hungerford et al. 1990). Fire scientists express heat flow as temperature profiles when explaining fire effects. They focus on the chemical, physical, and biological responses to specific temperatures. As part of this greenhouse study, I used thermocouples at three different depths to record temperatures both during and after the fire treatments in order to quantify temperatures to which the tansy ragwort seeds were exposed.

When moisture content is high in duff, heat from the surface fire may dry, ignite, and burn a portion of the duff (Ottmar et al. 1985). When duff is dry, smoldering is the

primary source of heat (except where there are large fuel concentrations) to the lower duff and mineral soil. Temperatures of smoldering duff reach 500 to 600 °C. Although duff temperatures are lower than flame (1000 to 1500 °C) during wildfire, the long duration of smoldering and close proximity of duff to the soil surface results in greater heating of the soil. Duff acts as a barrier to heat flow to the mineral soil when it does not burn during a wildfire (Frandsen and Ryan 1986). Thus, depending on both depth and moisture content of forest duff, fire can have variable effects on plant germination and emergence rate.

Burning can cause nutrients to be volatilized, transformed into highly available ions, or remain unchanged. These impacts are directly related to fire-caused temperatures. Temperature ranges and durations also influence survival of microorganisms, plant tissues, seeds, and roots. Plant tissue death occurs between 40 and 70 °C and seed death occurs between 50 and 120 °C. Nitrogen volatilization occurs between 300 and 500+ °C (Hungerford et al. 1990).

Soil temperatures recorded during grass burning are variable and depend on fuel distribution, moisture content, and prevailing weather conditions. Temperatures measured at the soil surface during grass fires range from 93 to 720 °C (Tothill and Shaw 1968). They rise rapidly, and then fall slowly over several minutes to near pre-burn levels. Increases in soil temperatures were less than 50 to 80 °C, were restricted to the top 3 – 4 cm of soil, and lasted only a few minutes (Raison 1979).

Slash and wildfires can expose soil to intense heat for long periods. Slash fires in U.S. Douglas fir habitat produce the highest temperatures immediately above and 2.5 cm

below the forest soil surface, 1004 and 320 °C, respectively (Isaac and Hopkins 1937). Temperatures are high enough during wildfires to kill seeds and other perennating organs of plants or at least alter their ability to grow. However, the variability in response to fire-mediated temperatures by different plant species necessitates testing on an individual species basis. The greenhouse experiment reported here was a burning and heating trial designed to determine the impact of the soil surface environment on tansy ragwort emergence rate.

Materials and Methods

Experimental Procedures

In August 2001, litter representative of areas in which tansy ragwort had invaded in northwestern Montana was collected from the Kootenai National Forest and brought back to the Plant Growth Center at Montana State University-Bozeman. Care was taken to collect litter at least 20 m from the nearest tansy ragwort population to avoid litter containing tansy ragwort seeds. The same volume of litter was collected from the forest for each sample. The litter was weighed prior to treatments and the number of sticks in various fuel size classes was tallied to quantify the fuel load per flat. Tansy ragwort seeds collected from the Kootenai National Forest in August 2001 were used in both the first and second run of this experiment. Prior to each run, the percent germination of the seed was tested in a growth chamber. Between runs, the seed was stored in a dark seed storage room where the temperature was 5 °C.

In this experiment seedling emergence in response to the following six treatments was observed: 1) seeds planted in soil beneath litter and no burning (litter), 2) seeds planted prior to burning litter (pre-burn), 3) seeds planted after burning litter (post-burn), 4) seeds planted into bare soil with no heat applied (bare soil), 5) seeds planted prior to heating bare soil (pre-heat) and 6) seeds planted after heating bare soil (post-heat). The reason for stratifying planting of seed pre- and post-burn was to separate the direct effects of burning on seed and the effect of changes to the soil and/or soil-litter interface environment on seed germination and emergence. The heated bare soil treatment was chosen to mimic the effect of flame passing over bare ground emitting radiant heat onto the soil.

Clean/pasteurized soil was spread in each of 32 steel 30.5 cm x 48.3 cm x 7.6 cm deep flats. Each of the six treatments was replicated eight times. Both the two burn treatments were created in eight flats, which were divided in half, as were the two heat treatments created in eight flats, one half receiving the "pre" treatment planting and the other half receiving the "post" treatment planting of tansy ragwort seed. For both the burn and the heat treatments, the entire flat was either burned or heated, depending upon treatment. All tansy ragwort seeds used in this experiment were collected in late August 2001 from the Kootenai National Forest. Wildfire temperature conditions at the soil surface were created using a propane torch to simulate flame and a radiant heater to simulate radiant heat from flame under a fumigation hood at the U.S. Forest Service Fire Science Lab in Missoula, MT. The experiment was first performed in February 2002 and repeated in September 2002.

Prior to the application of heat, 3 K-type thermocouples were placed in the flats at 0, 15, and 30 mm depths in the soil. The thermocouples were connected to a data logger to record temperature both during and after the application of fire and heat to the surface. The thermister value is actually a cold junction temperature recorded in bits. Thus, the bit value from the thermister was first converted to temperature then the 3 channel bits (0, 15, and 30 mm) were converted into temperature values with a polynomial formula. See Appendix E for the conversion polynomial formula.

For treatments 2, 3, 5 and 6, the steel flats were divided in half, one-half of which 100 tansy ragwort seeds were planted in the top 1 cm of soil prior to the burn or heat treatments. The litter was placed on the soil surface of eight flats and a hand-held butane torch was used to ignite the litter to create the burned litter treatments (2 and 3). For the heated bare soil treatment, no litter was placed on the soil and, just as in the burned litter treatment, 100 tansy ragwort seeds were planted 1 cm deep in the soil prior to the heat treatment. For each of the flats receiving the heat treatment, the radiant heater was placed 28 cm from the soil surface. The heater was allowed to run until the surface thermocouple reached 153 °C for 20 s and then was shut off. The data loggers recorded temperatures for both treatments for 2 hours following the application of heat. After the fire and heat-treated flats cooled (21 °C), 100 more tansy ragwort seeds were planted 1 cm deep in the second-half of the flats.

For treatment 1 (litter), 200 tansy ragwort seeds were planted 1 cm in the soil, then litter was placed on the soil surface 2 – 5 cm in depth. For treatment 4 (bare soil), 200 tansy ragwort seeds were planted 1 cm deep in the bare soil. Each of the 32 flats

were given 100 ml water and moved to cold storage (5°C) for 6 weeks to simulate winter conditions (stratification).

After the flats were removed from cold storage and placed in the greenhouse, they were watered as needed. If the soil surface was dry to the touch, they were watered. The exact amount of water was not quantified.

Data Collection

After 6 weeks in cold storage (5 °C) to simulate overwintering conditions, the flats were moved into a greenhouse where they received 14 hrs of supplemented artificial light and the average temperature was 21 °C. After 15 days, emerging tansy ragwort seedlings were counted once per week for 60 days, for a total of six repeated measures. Other vegetation that emerged in the flats containing litter was also recorded.

Statistical Analysis

Statistical analyses were performed with SAS 9.0 and Excel XP. The proportion of tansy ragwort seedlings that emerged per treatment over time was first analyzed qualitatively. The number of emerged seedlings was found to decline after 30 days in the greenhouse. Because emerged tansy ragwort plants were not marked, a mortality rate could not be calculated. Therefore, statistical analyses were performed on the first two counts of emerged seedlings in time, at 15 and 25 days for the first run of the experiment, and at 22 and 29 days for the second run.

Because the response variable emergence can be considered a binomially distributed attribute, it was transformed to the logit scale. The transformed data was

tested for normality by plotting the residuals. The residuals fit a straight line, indicating that the quantiles fit a normal distribution. This was supported by the probability associated with the Shapiro-Wilk test statistic for the first run ($W = 0.91$; $P < W = 0.0001$) and the second run ($W = 0.69$; $P < W = 0.0001$). The transformed data also met the homogeneous variance assumption as tested by plotting the predicted values against the residuals. These results indicated that it would be appropriate to use the generalized linear mixed models procedure to test for main treatment effects (soil surface heat or no heat).

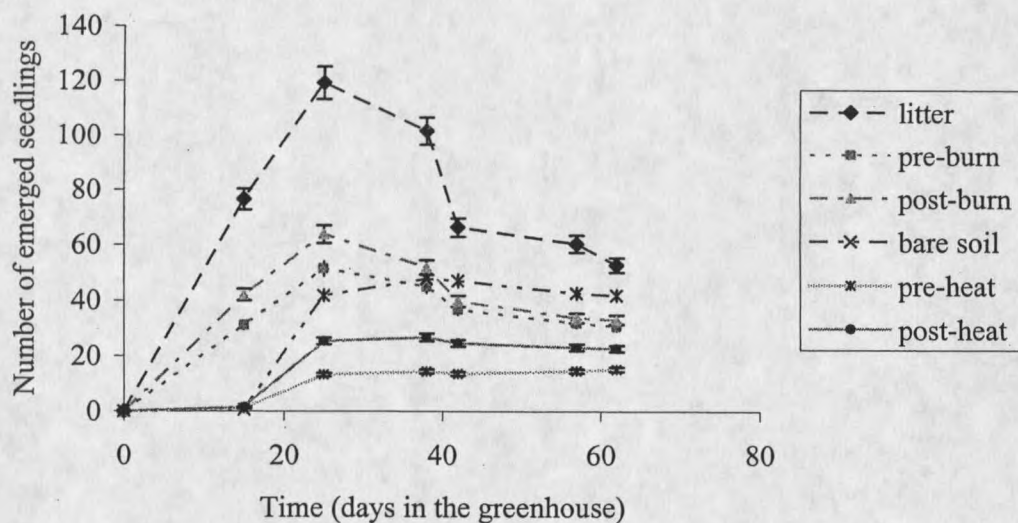
The objective of this experiment was to determine the effect of six soil surface treatments on tansy ragwort seedling emergence rate. The response variable of interest was the proportion of seedlings that emerged per treatment. Least-squares means (LS-means) of fixed effects were computed for the model. Tukey's adjustment was used for a multiple comparison adjustment for the p-values and confidence limits for the differences of LS-means. The Tukey procedure permits the family confidence coefficient and the family α risk to be controlled (Neter et al. 1996).

Results

Treatment Differences

All treatments with the litter component had a higher number of initially emerged seedlings than any bare soil treatments, for both runs of the experiment (Figure 13). In the first and second runs of the experiment, the highest number of seedlings emerged in the unburned litter (litter) treatment.

A: First run



B: Second run

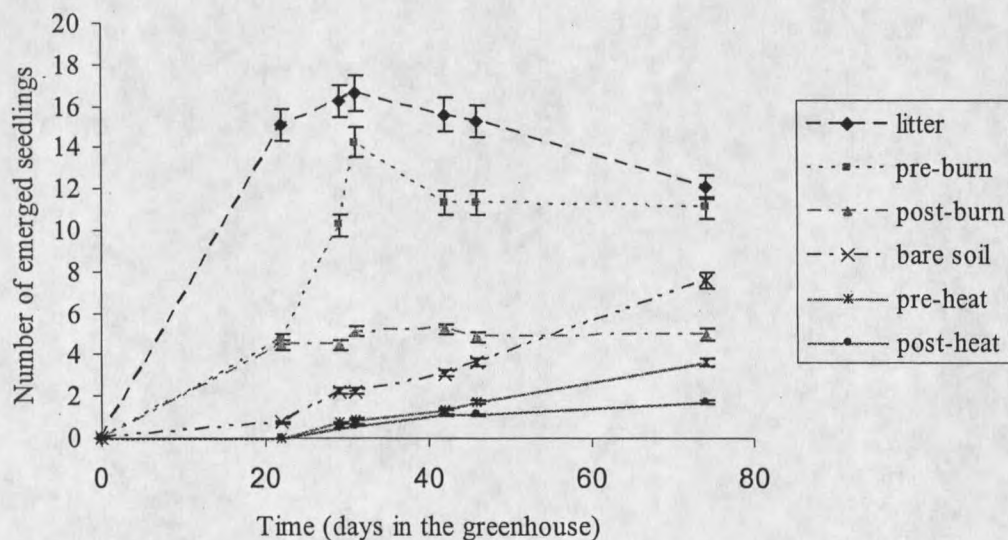


Figure 13. Mean number and standard error ($n = 8$) of emerged tansy ragwort seedlings out of 100 seeds planted (200 for the litter and bare soil treatments) in six treatments over 62 days following placement in the greenhouse for the first run (A) and over 74 days following placement in the greenhouse for the second run (B) of the experiment.

The second highest number of seedlings emerged in the post-burn treatment, where seeds were planted after burning (post-burn) in the first run, whereas in the second run flats where seeds were planted prior to burning (pre-burn) had the second highest number of emerged seedlings. Since emerged tansy ragwort plants were not marked, mortality rate was unknown. The number of emerged seedlings began to decline after 30 days. Thus, the ANOVA for treatment effects was conducted on emerged seedling counts at 15 and 25 days for the first run and at 22 and 29 days for the second run before mortality began to occur.

For the first run of the experiment, the treatment effect ($P < 0.0001$) and the time effect ($P < 0.0001$) were significant, as well as the treatment by time interaction effect ($P > 0.0013$). The treatment, time, and interaction effects were also all significant for the second run ($P < 0.0001$, $P > 0.0003$, $P > 0.0218$, respectively).

The three treatments containing litter (litter, pre-burn, post-burn) were not significantly different from each other at 15 days in the first run of the experiment ($P > 0.05$) (Figure 14). Likewise, the three bare soil treatments (bare soil, pre-heat, post-heat) were not different in the first run of the experiment ($P > 0.05$). The three litter-containing treatments had higher emergence rates than the three bare soil treatments ($P < 0.05$) at 15 days. Similar results occurred at 25 days; however, the pre-burn treatment was not, in this case, different from the post-heat treatment ($P > 0.05$).

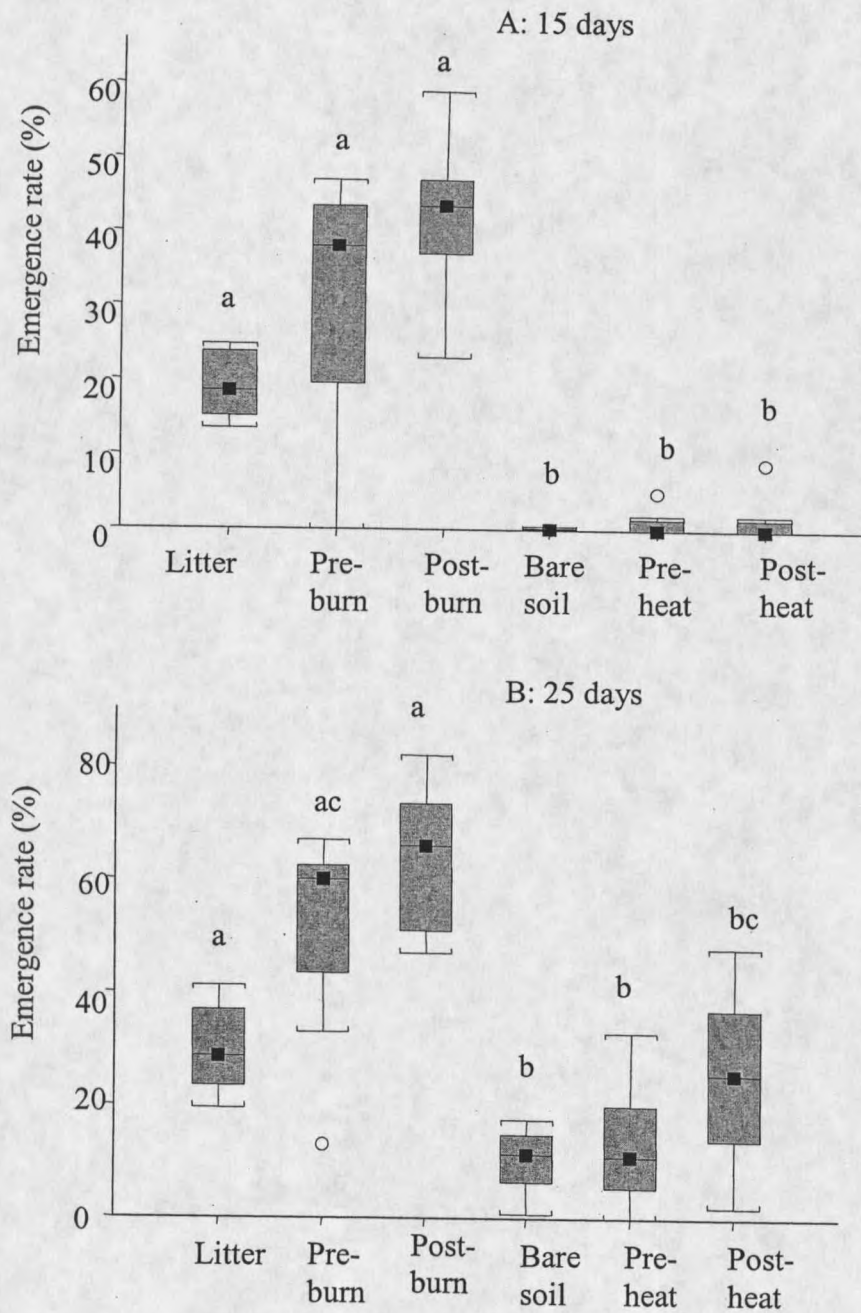


Figure 14. Median (black box) emergence rates, 50% of data (light shaded box), all of data (whiskers) other than outliers (circles) of tansy ragwort seedlings for the first run of the experiment at 15 days (A) and 25 days (B). Boxes with the same letter indicate that means calculated from the transformed data (explained in the text) were not significantly different at $\alpha = 0.05$.

The second run of the experiment was similar to the first, except that the emergence rate was lower. At 22 days emergence in all litter-containing treatments (litter, pre-burn, post-burn) was higher than in bare soil treatments (bare soil, pre-heat, post-heat) ($P < 0.05$) (Figure 15). Results were similar at 29 days, although emergence in the post-burn, bare soil, and pre-heat treatments was not significantly different ($P > 0.05$).

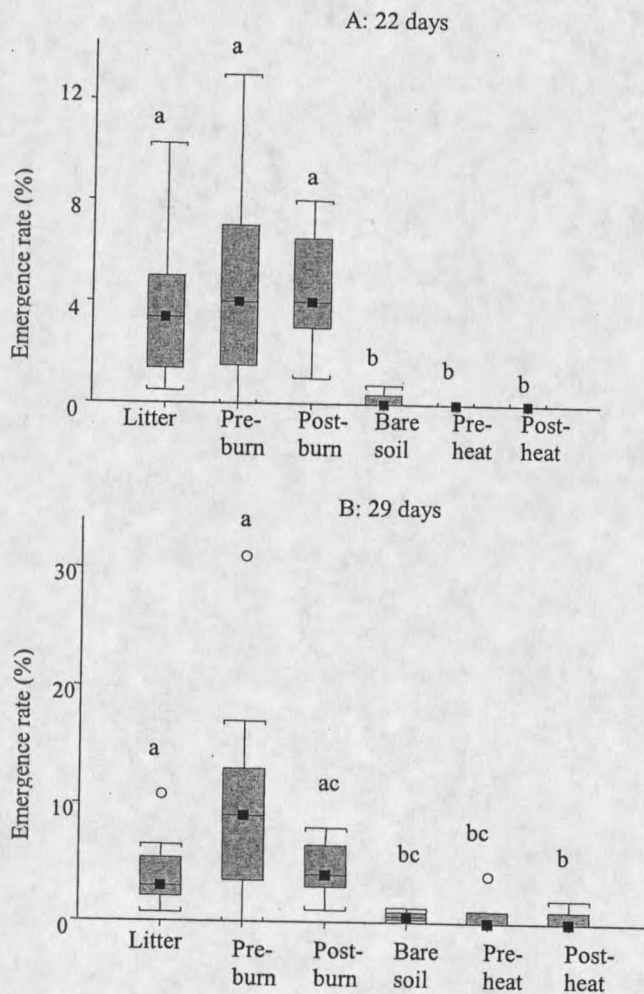


Figure 15. Median (black box) emergence rates, 50% of data (light shaded box), all of data (whiskers) other than outliers (circles) of tansy ragwort seedlings for the second run of the experiment at 22 days (A) and 29 days (B). Boxes with the same letter indicate that means calculated from the transformed data (explained in the text) were not significantly different at $\alpha = 0.05$.

Temperatures

In the first run of the experiment, the highest temperature reached on the surface (0 mm) for the pre-burn and post-burn treatment was 433 °C, while the lowest was 162 °C (Table 14). The highest recorded temperature at 15 mm, near where the seeds were buried (1 cm), was 62 °C and the low was 29 °C. Below where the seeds were buried, at 30 mm, the highest temperature was 46 °C. A similar range of temperatures was reported for the burned treatments in the second run of the experiment with a high of 450 °C and a low of 247 °C at 0 mm. The highest temperature at 15 mm in the second run was also 62 °C. At the 30 mm depth, the high temperature was 46 °C.

For the radiant-heated bare soil treatments, the temperature spread was narrower than for the burned treatments with a high of 192 °C and a low of 164 °C at 0 mm (on the soil surface). This is similar to the second run of the experiment, where the high was 174 °C and the low was 156 °C at 0 mm. The highest recorded temperature at 15 mm for the first run was 62 °C and for the second run it was 59 °C. At 30 mm, for the first run the high was 34 °C and for the second run, the high was 31 °C.

Table 14. Highest (High) and lowest (Low) of the high temperatures (°C) recorded at 0, 15, and 30 mm in the burned litter treatments and the bare soil heated treatments.

	Burned litter treatments						Bare soil heated treatments					
	First run			Second run			First run			Second run		
	0	15	30	0	15	30	0	15	30	0	15	30
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
High	433	62	46	450	62	46	192	62	34	173	59	31
Low	162	29	34	247	28	40	164	29	31	156	28	27

Discussion

More tansy ragwort seeds emerged in the three treatments containing litter than in bare soil treatments. Thus, there was evidence to reject the null hypothesis. However, the outcome of this study was somewhat contrary to what was expected. In Meijden and Waals-Kooi's study (1979), tansy ragwort germination and survival were consistently higher in cleared plots than in undisturbed plots, which they explained as suppression of seedlings by dense vegetation cover. In the present study, emergence rates were lower in bare soil treatments than in treatments with litter covering the bare soil. This suggests that relative air humidity near the soil surface may have remained higher in the litter treatments, thereby preventing soil drying and promoting seed germination and emergence.

Although the overall seedling emergence patterns over time were similar for the first and second run of the experiment, the number of emerged seedlings was considerably lower in the second run. This may be attributable to the fact that the first run was performed in the spring from April to June. In the spring days length is considerably longer and thus the treatments in the greenhouse received more natural light than the treatments in the second run of the experiment, performed in the fall from November to January. This difference in number of emerged seedlings could also be explained by the use of older seed for the second run of the experiment. However, the seed was tested for percent germination in a growth chamber prior to both the first and second runs. Both germination tests had a mean percent germination rate of 70%. The median percent germination for the test prior to the first run was 75% and the 70% prior

to the second run. Thus, the median percent germination rate was 5% lower for the second run.

Regarding length of daylight, the effect of photoinduction on flowering has been studied for tansy ragwort (Prins et al. 1990). Results show that control of flowering in tansy ragwort is relatively complex. This species has both a threshold size requirement for vernalization and photoinduction (Prins et al. 1990). However, results are not yet available detailing the effect of day length on seed germination and emergence.

Light is required by tansy ragwort for germination. Meijden and Waals-Kooi (1979) showed that coverage by sand to a depth of more than 4 mm led to reduced light transmission and enforced dormancy in the achenes. Experiments with achenes of British tansy ragwort populations (Wesson and Wareing 1969b, a) showed that although light promoted germination, a proportion of the achenes germinated in darkness after a 20-week period of dry storage. By contrast, the achenes from the dune area from Meijden and Waals-Kooi's (1979) study still had almost complete inhibition of germination in total darkness after 3 years of storage.

Similar burn temperatures were achieved for the first and second runs of the experiment across treatments. Seed death occurs between 50 and 120 °C (Hungerford et al. 1990). Temperatures within and above this range were recorded for both the burned and heated bare soil treatments at 0 mm and 15 mm. Therefore, it is probably that some tansy ragwort seeds were heat-killed in the pre-heat treatment flats and perhaps explains why fewer seedlings emerged in the heated bare soil treatments.

No studies have yielded conclusive results indicating tansy ragwort's response to burning (Poole and Cairns 1940, Mastroguiseppe et al. 1982). However, both observations of natural floras and experimental studies indicate that tansy ragwort is more closely associated with disturbed sites where vegetation cover was reduced and bare soil exposed (Watt 1987b, McEvoy and Rudd 1993, McEvoy et al. 1993). Grazing and mowing have been shown to provide a favorable environment for the establishment of tansy ragwort (Meijden and Waals-Kooi 1979, Watt 1987b, McEvoy and Rudd 1993, McEvoy et al. 1993). The present study, particularly the first run, indicates that the burning of litter may also contribute to a more favorable environment for tansy ragwort emergence.

Fire may improve soil surface conditions for tansy ragwort emergence by increasing initial levels of available nitrogen. Studies have shown soil nitrogen levels to be higher immediately following fire, but that losses of N occur through volatilization during fire. Choromanska and DeLuca (2001) found that total N, potentially mineralizable N (PMN), $\text{NH}_4(+)\text{-N}$, and $\text{NO}_3(-)\text{-N}$ concentrations in surface (0-10 cm) mineral soils were significantly higher immediately after wildfire. Potentially mineralizable N decreased significantly on all fire-exposed sites from 9 months to the end of the study period (21 months) (Choromanska and DeLuca 2001). Fire effects on soils and nutrient cycling have been reviewed extensively. Such effects include losses of N through volatilization during fire (DeBell and Ralston 1970), transfer of ammonium from the forest floor to the mineral soil (Covington and Sackett 1992), and changes in mineralization kinetics (Prieto-Fernandez et al. 1993). Surface soil exchangeable base

cation concentrations were found to increase due to ash deposition with a simultaneous increase in pH and nutrient losses through leaching (Bayley et al. 1992, Williams and Melack 1997). Fire consumption of the forest floor may lead to a decrease in soil nutrient reserves (Groeschl et al. 1993). Of course, inferences of these effects must take into account site and landscape heterogeneity making each situation unique.

Wildfires in northwestern Montana usually occur in late summer and early fall – a time of the year when few tansy ragwort seeds germinate. However, studies show that the amount of nitrogen and other nutrients in the soil decreases with time following wildfire (Choromanska and DeLuca 2001). Therefore, nitrogen availability in the spring following a wildfire may be lower than normal due to volatilization and leaching.

Slash pile burns usually occur in late winter and early spring, a time of year when most tansy ragwort seeds germinate. Perhaps the slash burns produce an initial boost in N to the soil that causes an increase in tansy ragwort seed germination and emergence. Watt (1987b) showed that ten months after sowing, seedlings of tansy ragwort persisted in the high nitrogen environment of ex-cow-dung patches. This finding indicates that tansy ragwort responds favorably to increased nitrogen levels. Watt (1987c) investigated the effects of a high or low level of nitrogen fertilizer and the presence or absence of a grass-suppressing herbicide (propyzamide) on the establishment of tansy ragwort in three sizes of bare soil patch in a perennial ryegrass sward. Seedling emergence in the field was higher in the largest patches, but in the boxed swards most seedlings emerged in the smallest patches, maybe because these patches were less susceptible to desiccation. It is possible that the highest number of seedlings emerged in litter-containing treatments of

the present experiment because they were more protected from desiccation than seedlings in the bare soil treatments.

Furthermore, Watt (1987c) found that tansy ragwort seedling emergence was higher in high nitrogen plots in the field. Such rapid seedling emergence occurred in boxed swards only when treated with both propyzamide and nitrogen, available as a result of the reduced competition for the more limited supply of nitrogen in this more readily leached environment.

The emergence phase of seedlings might be especially sensitive to environmental extremes. The non-burned and bare soil treatments likely had a lower level of available nitrogen than the litter and burned treatments because of the lack of plant and woody debris and the lack of burned litter. In addition, the bare soil treatments were more exposed because they were not buffered by a litter layer, making them prone to faster soil drying. Because they lacked an insulating litter layer, the bare soil treatment flats may also have had greater fluctuations in temperature. In addition to providing insulation and protection, the litter layer in the burned treatments formed small gaps through which light could penetrate, encouraging tansy ragwort germination and emergence.

The importance of moisture to tansy ragwort germination was demonstrated in a study comparing seedling densities on north- and south-facing slopes in Britain. Hillier (1984) studied the number of natural tansy ragwort seedlings establishing in gaps of different sizes. In autumn, seedling densities were highest in large gaps on the north-facing slope and in small gaps on the south-facing slope. This response was explained by

smaller gaps that provided more protection from water loss in the shallower soil under summer drought conditions on the south-facing slope.

Dry conditions at the soil surface have been shown to decrease tansy ragwort germination. Meijden and Waals-Kooi (1979), demonstrated that a thin coverage of sand (1-2 mm) stimulated germination compared with uncovered achenes, due to more favorable moisture conditions. They found that temperature, soil moisture, and ambient humidity have an important influence on the timing and level of tansy ragwort germination. Short periods of frost or drought following wetting of the achenes may induce dormancy. High temperature, low soil moisture and low air humidity reduced the capacity for germination even after transfer to more favorable environments (Meijden and Waals-Kooi 1979).

If the treatments in the current study were repeated, soil analysis should be performed both before and after the burning and heating treatments to quantify forms of nitrogen and other soil nutrients present. Also, temperature at the soil surface should be recorded for the duration of the study while the tansy ragwort seeds are emerging to better quantify temperature oscillations at the surface under different amounts of litter caused by the treatments. If possible, relative humidity should also be quantified at the soil surface. It would also behoove future researchers to grind the litter prior to the burn treatments. Grinding the litter prior to the burn treatments would ensure a standardized quantity and homogenized composition of material, resulting in a more even burn, eliminating "hot spots" on the soil surface. While this would not mimic how real wildfire

behaves, it would ensure that the tansy ragwort seeds are all subjected to similar conditions.

This work illustrates how different soil surface environments affect tansy ragwort emergence. These results represent a first step in gaining a better understanding of where to expect invasive populations of tansy ragwort to emerge in fire-affected areas.

Expanding the work described here to include the quantification of more variables could aid land managers in prioritizing tansy ragwort management and predicting the effects of wildfire on the plant community in areas where tansy ragwort is known to be present.

The greenhouse experiment reported here was a burning and heating trial. The results indicate that tansy ragwort emergence rates are higher in litter-covered soil, burned, or unburned environments versus bare soil or heated bare soil environments. The results may parallel previous findings showing that tansy ragwort emerges and establishes faster in environments with high N levels, ambient humidity, small oscillations in soil temperature, and light. The findings do not fully explain the observation that tansy ragwort densities are higher following wildfire or are often present where slash burns occurred. Previous studies quantifying the amount of nitrogen and nutrients available to plants immediately following fire indicate that levels are higher initially and then tend to decrease with time. To more fully understand the results of the present study, the experiment should be repeated. Quantification of levels of nitrogen and other soil nutrients may help to determine if tansy ragwort seeds in the burned treatments were exposed to higher levels of nitrogen, thereby explaining the observed increase in burned treatment emergence rates.

THE EFFECTS OF TEMPERATURE ON TANSY RAGWORT SEED GERMINATION

Introduction

Germination and seedling establishment are critical stages in the life cycle of any plant. Restrictions of species to certain soils, elevations, communities, and densities may be the result of rigorous selection pressure exerted mainly during these early developmental life stages. Montana tansy ragwort infestations are of particular significance because this weed was previously thought to occur primarily in maritime climates. Northwestern Montana was considered resistant to tansy ragwort invasion mainly due to prolonged low temperature in winter, low soil moisture, and low air humidity, which reduce tansy ragwort's capacity for germination. Soil drying has been shown to decrease tansy ragwort germination (Meijden and Waals-Kooi 1979).

This experiment was conducted to address germination of tansy ragwort in response to temperature gradients. The major objective of this study was to determine the optimum and range of temperatures where tansy ragwort seed will germinate. In addition, we sought to verify that seed collected from Montana populations responded to temperature similarly to seeds tested by Meijden and Waals-Kooi (1979) in the Netherlands and Baker-Kratz and Maguire (1984) in Washington. The germination rate of tansy ragwort seeds placed at different points along a temperature gradient plate was observed for four weeks. Our null hypotheses were that the optimum temperature for germination would be 20 °C, that the range for germination would be 5 °C to 30 °C, and

that the shape of the germination-temperature response curve would also be the same as found by Meijden and Waals-Kooi (1979) and Baker-Kratz and Maguire (1984).

Materials and Methods

General

All disk achenes used in the experiments were collected in August 2001 approximately 60 miles southeast of Libby, MT, from stands of tansy ragwort growing on the Kootenai National Forest where winters are generally cloudy, cool, and wet. Annual precipitation averages 57 cm, most of it occurring from November to January. In the summer, days are warm and dry and nights are cool. However, climatic conditions in this mountainous area are extremely variable over short distances due to local topographic effects (Kuennen and Nielsen-Gerhardt 1995). "Frost-pockets" are an example of a local topographic effect, where cold air is trapped in low areas on summer nights causing frequent summer frosts.

In contrast, the tansy ragwort seeds used by Baker-Kratz and Maguire (1984) were collected 16 km east of Olympia, WA where annual precipitation averages 129.4 cm, most of it occurring from October to March. The area's climate is characterized by warm, generally dry summers and mild, wet winters.

The tansy ragwort populations and seeds studied by Meijden and Waals-Kooi (1979) in The Netherlands were located in the coastal dunes of Meijndel, north of The Hague in very calcareous soils. This area has a temperate maritime climate influenced by the North Sea and Atlantic Ocean. Rainfall is distributed fairly evenly throughout the

year with average annual precipitation exceeding 700 mm. Average temperature ranges are from -1 to 4 °C in January to 13 to 22 °C in July.

Germination-Temperature Relations

Individual, mature capitula were collected from a random sample of 65 plants across a 5 km² area representing my study site (see description in Chapter 2). Optimum constant temperature was determined for the disk achenes. The achenes were removed from the capitula, pooled, and then separated into ray and disk types. The pappi and corollas were removed from all achenes prior to germination to make handling of the seeds easier and decrease the risk of the seeds blowing away.

Sixty achenes were placed on a temperature gradient plate at 9, 15, 20, 25, 30, and 35 °C (10 disk achenes per temperature). Only 10 achenes were used per temperature per replication due to space limitations on the plate. Achenes were placed on chromatography paper moistened with distilled water in covered temperature gradient plates. The test was conducted under constant temperature with alternating 12 h light/12 h dark conditions. The light intensity was 20 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ obtained from cool white fluorescent bulbs. Achenes were considered germinated when both the radicle and cotyledons emerged. The germination test was continued for 31 days which included a 2 week period at the end where no further germination took place. In this study counts were made every day for the duration of the experiment.

Statistical Analysis

Statistical analyses were performed with SAS 9.0 and Excel XP. The response variable of interest was the proportion of seeds that germinated per temperature interval. The three data sets (Montana, Washington, and The Netherlands) were each fit to a nonlinear regression model. The dependent variable was germination rate and the independent variable was temperature. The functional fit to each data set was $Y = ab^{(x-c)^2}$ (Sit and Poulin-Costello 1994), where a is the peak of the curve (maximum germination proportion), b is a shape parameter defining the width of the curve, and c is temperature corresponding to the peak (optimum germination temperature). Y was the proportion of germinated seed at X temperature ($^{\circ}\text{C}$). The model was fit with PROC NLIN (SAS 9.0 2003). Starting values of the parameters were specified as were the derivatives of the model with respect to the parameters. The parameters in the model were estimated by the least squares method. A plot of the residuals indicated that they were normally distributed. This was supported by the probability ($P < W = 0.0005$) associated with the Shapiro-Wilk test statistic ($W = 0.81$ to 0.89) for all three data sets. A plot of the residuals versus the predicted values indicated that the assumption of homogeneous variance was also met.

Results

Temperature and Rate of Germination

Percent germination of disk achenes was highest at 20°C for all populations from Montana, Washington, and the Netherlands (Table 15). In the Montana population, disk

achenes had the lowest germination at 30 °C and no achenes germinated at 35 °C. The germination percent was higher at 30 °C for the Washington and Netherlands seeds than the Montana seeds.

Table 15. Mean percent germination of tansy ragwort disk achenes after 31 days and 2 weeks elapsed without further germination.

Temperature (C)	Germination (%)		
	Montana	Washington ^a	The Netherlands ^b
5	-	2	0
9	5	-	-
10	-	72	68.5
15	70	83	76.5
20	70	85	85.5
25	42.5	63	45
30	2.5	11	8
35	0	-	-

^a Data obtained from Baker-Kratz and Maguire 1984

^b Data obtained from Meijden and Waals-Kooi 1979

The germination curves for each of the four replications of the Montana seeds were similar and indicate optimum germination occurs at 15 to 20 °C (Figure 16).

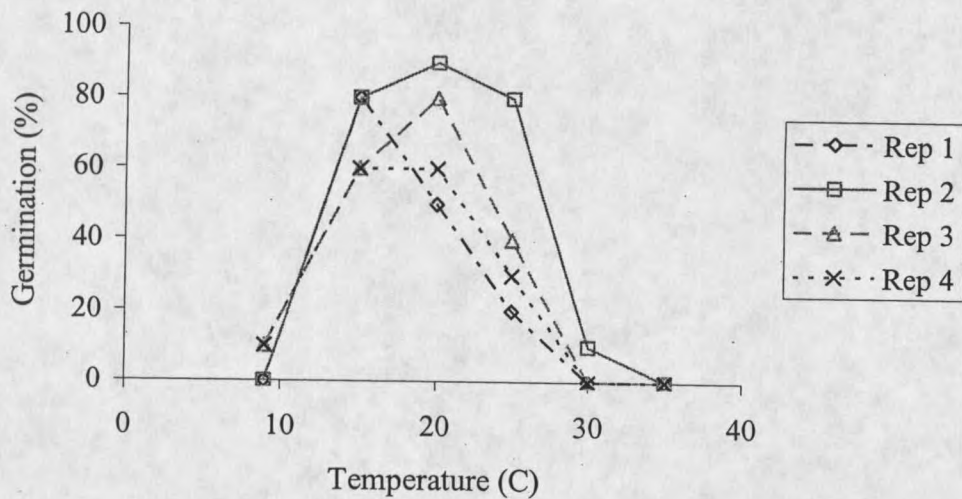


Figure 16. Percent germination of tansy ragwort disk achenes, collected in Montana, by replication after 31 days. $n = 10$ seeds per temperature.

The germination curves for the Washington and The Netherlands seeds are similar to each other, as well, indicating that optimum germination occurs at 20 °C (Figure 17).

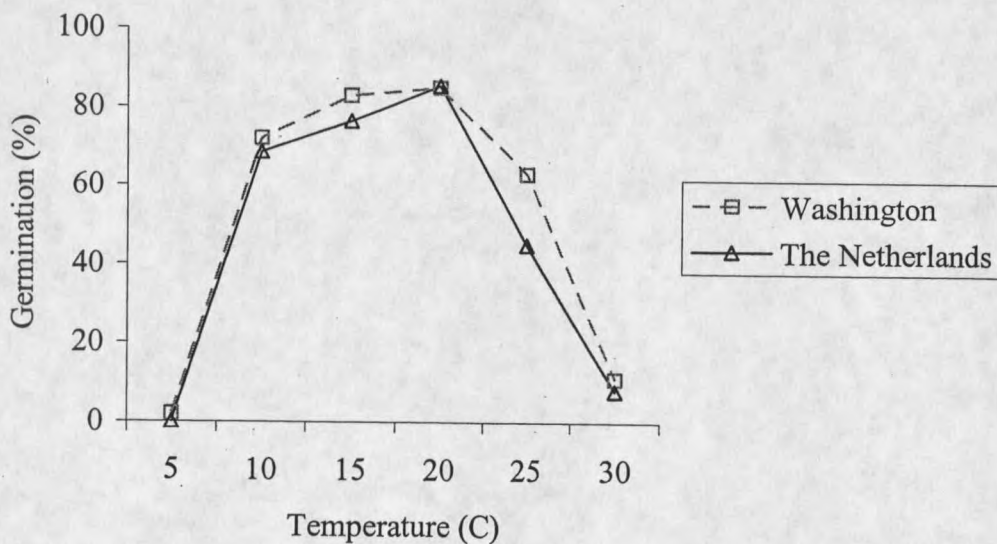


Figure 17. Mean percent germination of tansy ragwort disk achenes collected in Washington and The Netherlands after 15 and 40 days, respectively. Washington: $n = 100$; The Netherlands: $n = 50$.

The model was significant for the Montana germination data ($P < 0.0001$, $F = 69.52$, $df = 3$), the Washington data ($P > 0.0117$, $F = 26.46$, $df = 3$), and The Netherlands data ($P > 0.0116$, $F = 26.56$, $df = 3$). The response curves for each of the three data sets are very similar (Figure 18).

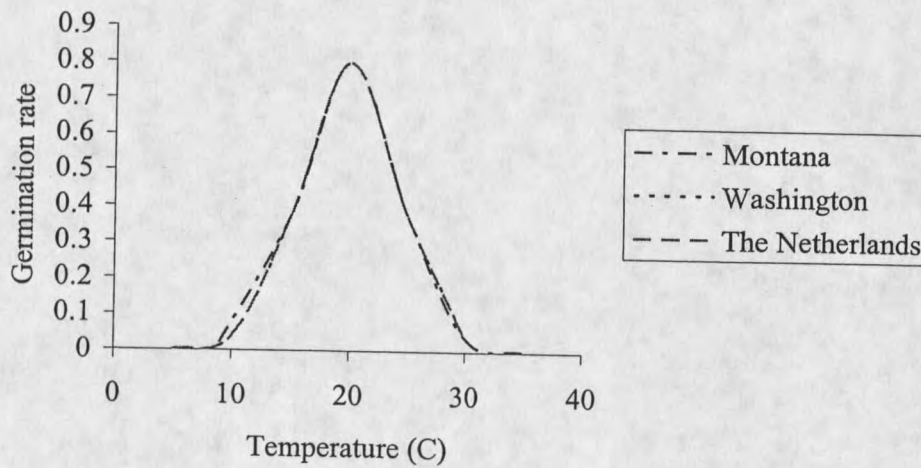


Figure 18. Response curves of tansy ragwort germination rates for seed collected from Montana, Washington, and The Netherlands.

The parameters a , b , and c were quite similar for each of the three germination data sets (Figure 4). For each parameter, the 95% confidence limits overlapped between populations. Parameter a has a slightly narrower confidence limit for the Montana population than the Washington and Netherlands populations. However, the confidence limits do overlap indicating that no significant difference exists between the populations.

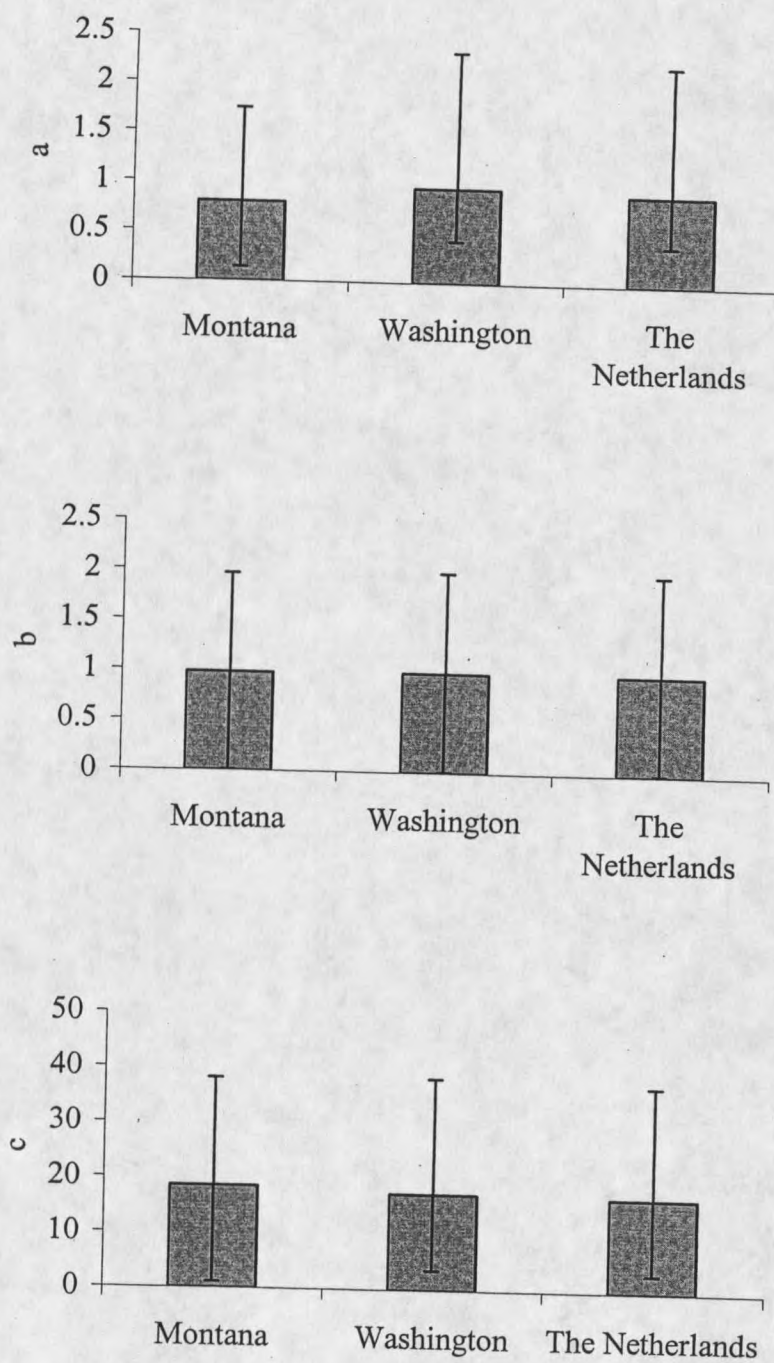


Figure 19. The estimated parameter values *a*, *b*, and *c* and 95% confidence intervals from non-linear regression analysis for seeds collected from Montana, Washington, and The Netherlands.

We could not reject the null hypothesis that the optimum temperature for tansy ragwort germination was 20 °C, that the range for germination was 5 °C to 30 °C, and the response curve shapes (*b*) were the same for the Montana, Washington, and The Netherlands populations (Meijden and Waals-Kooi 1979, Baker-Kratz and Maguire 1984). In addition, the maximum proportional germination (*a*) was the same for each population.

Discussion

The temperature gradient plate study tested whether tansy ragwort seeds collected in Montana responded to temperature the same as those collected from Washington and The Netherlands. We found that Montana seeds do respond similarly to temperature as the seeds from the other locations that have wetter, milder, and more humid environments. A qualitative examination of the Montana germination results shows that there may be a wider optimum germination (15 °C and 20 °C) in the Montana tansy ragwort seed population. However, the model showed that no differences exist between the optimum temperatures for the three populations.

The lack of difference in germination response to temperature across populations raises the question of whether genotypic variability and phenotypic plasticity are factors in the success of tansy ragwort as an introduced species. Invasive plants such as tansy ragwort are often more vigorous in their introduced ranges than in their native ranges. This may be due to an innate superiority of plants from some habitats or an escape from their natural enemies (Wolfe 2002). An alternative hypothesis is that invasive plants

evolve increased competitive ability in their introduced range (Willis et al. 2000, Siemann and Rogers 2001). Clearly, germination response to temperature has little variability across populations that would help explain its success in widely divergent environments.

Willis et al. (2000) tested the hypothesis that the increased size of certain weed species was genetically, rather than environmentally, based. A common environment growth experiment revealed no significant differences in the size of *Carduus nutans*, *Digitalis purpurea*, *Echium vulgare*, or *Senecio jacobaea* (tansy ragwort) sampled from alien (Australia and New Zealand) or native (Britain and continental Europe) habitats. They concluded that post-invasion genetic changes associated with increased size may be unusual and that the phenomenon, where it occurs, generally reflects a plastic response to a new environment.

Siemann and Rogers (2001), on the other hand, did find genetic differences for invasive trees with different growth rates. They performed a common garden experiment with Chinese Tallow Tree (*Sapium sebiferum*) that showed invasive genotypes were larger than native genotypes, and that the invasive genotypes were more likely to produce seeds, but had lower quality and poorly defended leaves against herbivory.

Future work could involve collecting more seeds from tansy ragwort's native environment and environments in which tansy has been introduced for a long time (over 50 years) and for a short time (less than 20 years). More replications may more adequately test whether differences exist between optimum germination temperatures in

tansy ragwort's native and introduced environments, to test for higher phenotypic plasticity in introduced populations.

In addition, tansy ragwort seeds and plants could be collected from the Oregon Coast, thought to be the source of the Montana populations, to compare the Oregon population with the Montana population using reciprocal transplant studies of growth as well as germination and emergence. A common garden experiment could be established with tansy ragwort from its native range (Europe, Asia, and Siberia), place of introduction to North America (Nova Scotia), and areas colonized over a century later in Montana and Oregon. These experiments would allow us to compare populations as well as physiological and perhaps life-history differences between native plants and post-invasion plants. This research may also lend some insight as to why or how tansy ragwort is invasive in Montana. Alternatively, the comparison may reveal no differences (Willis et al. 2000). There is little consistent evidence that genetic adaptations and/or phenotypic plastic responses may contribute to the success of invasive species. This inconsistency continues to make it difficult to predict new problem species.

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APPENDICES

APPENDIX A
TRANSITION PARAMETER VALUES ACROSS
ENVIRONMENTS

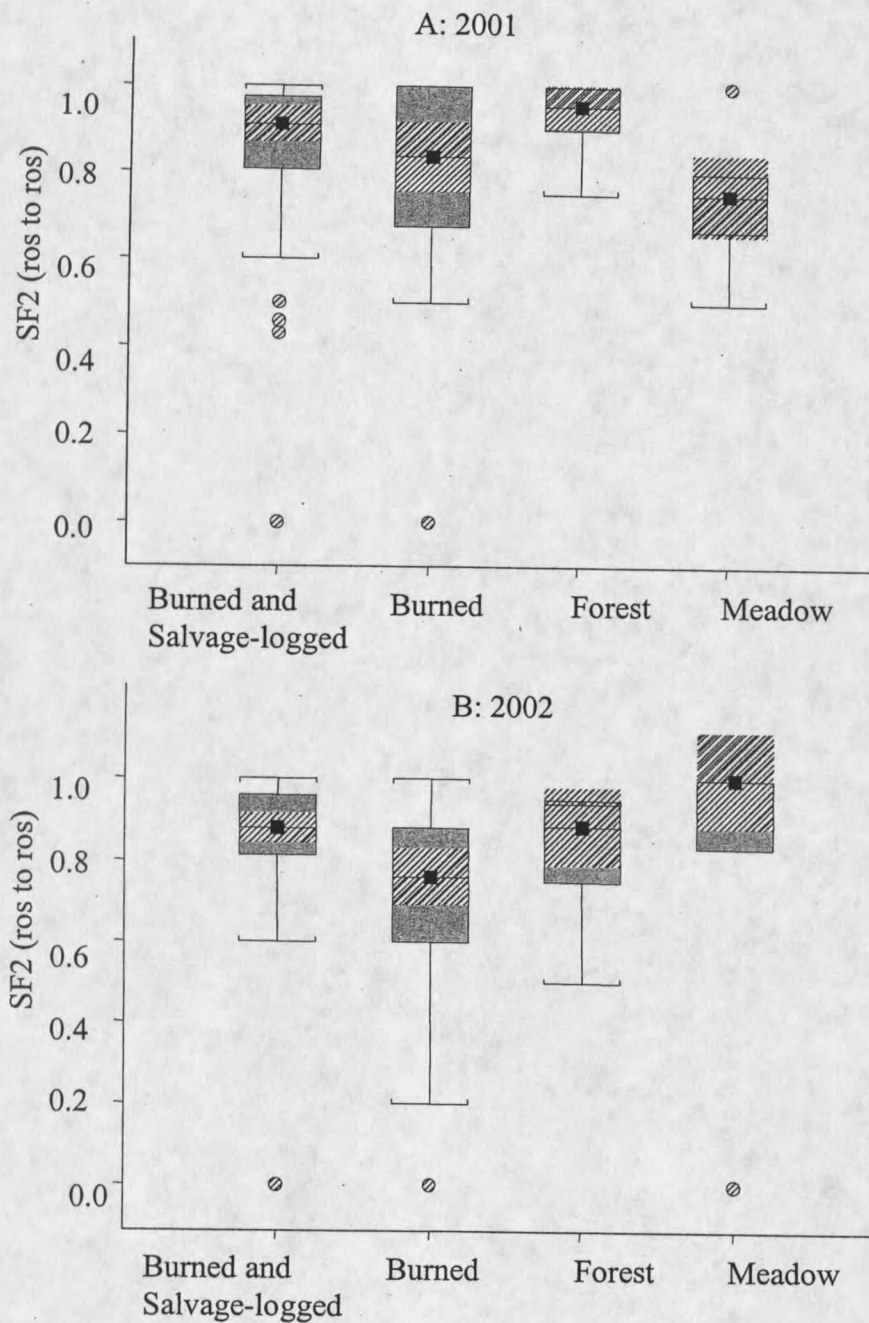


Figure 20. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

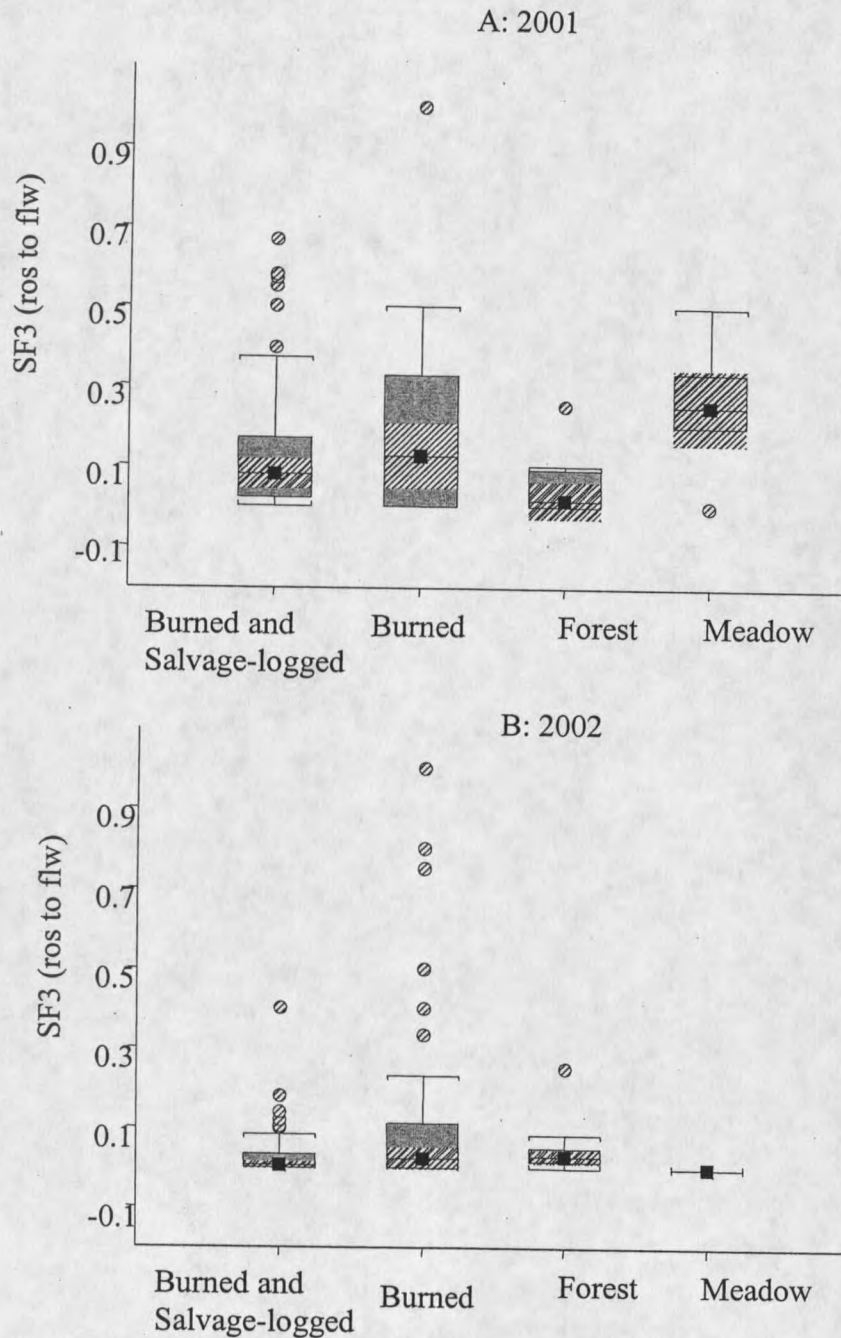


Figure 21. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

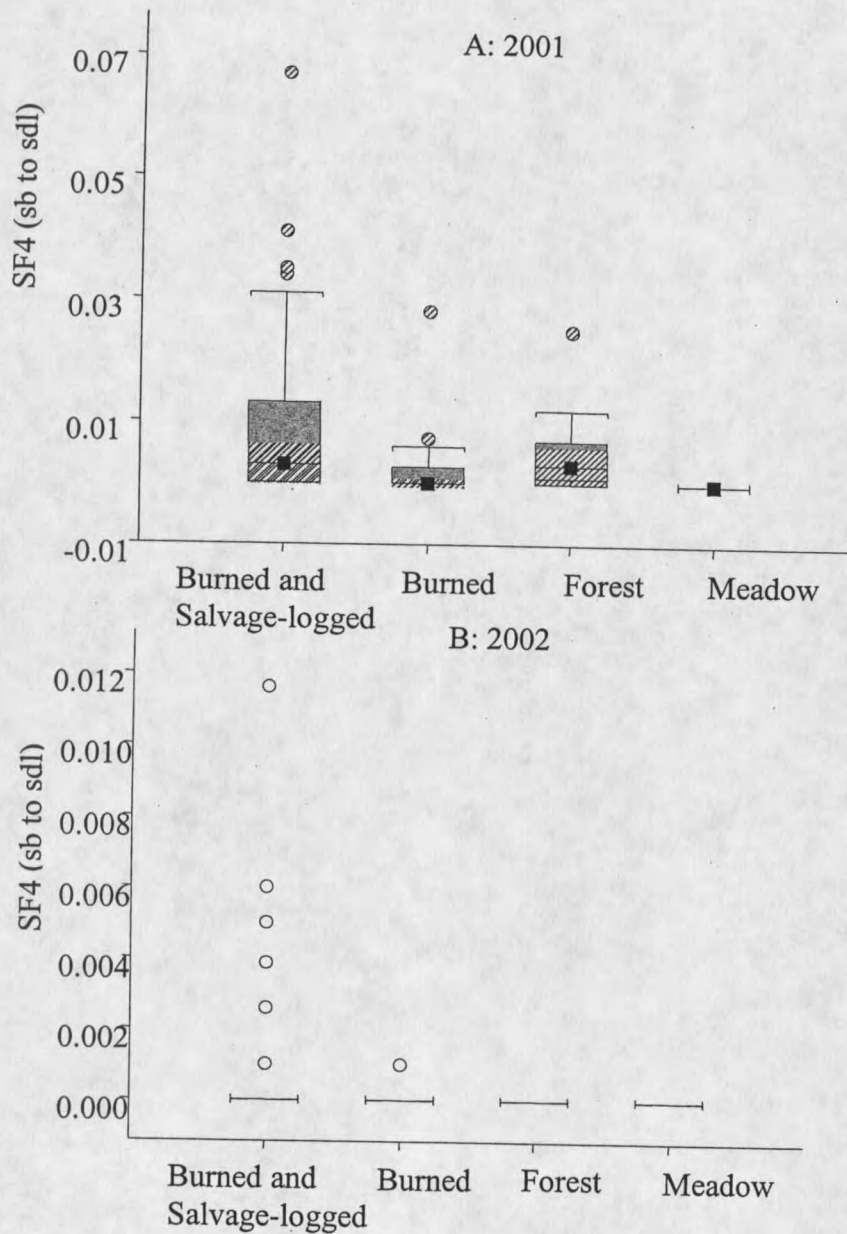


Figure 22. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

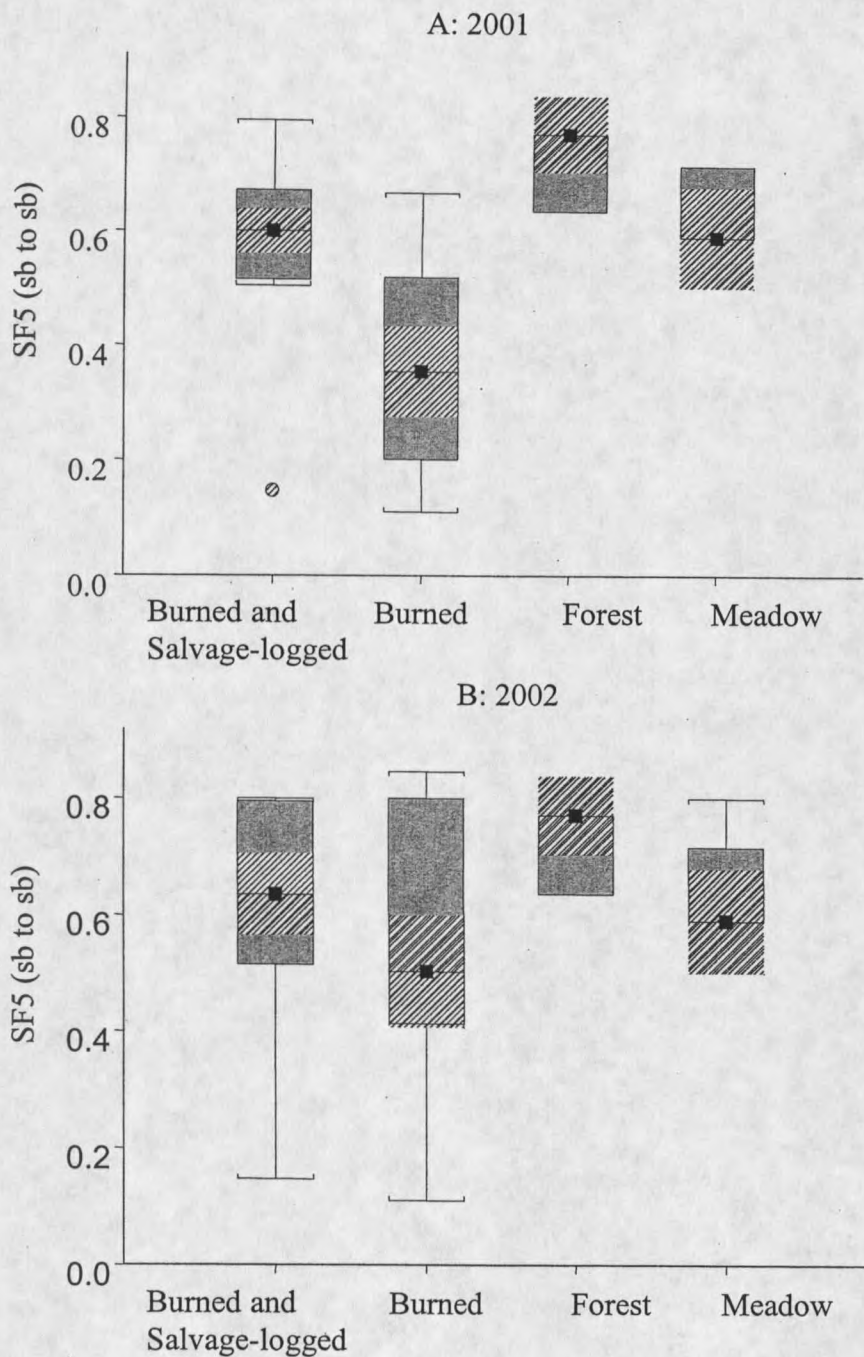


Figure 23. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

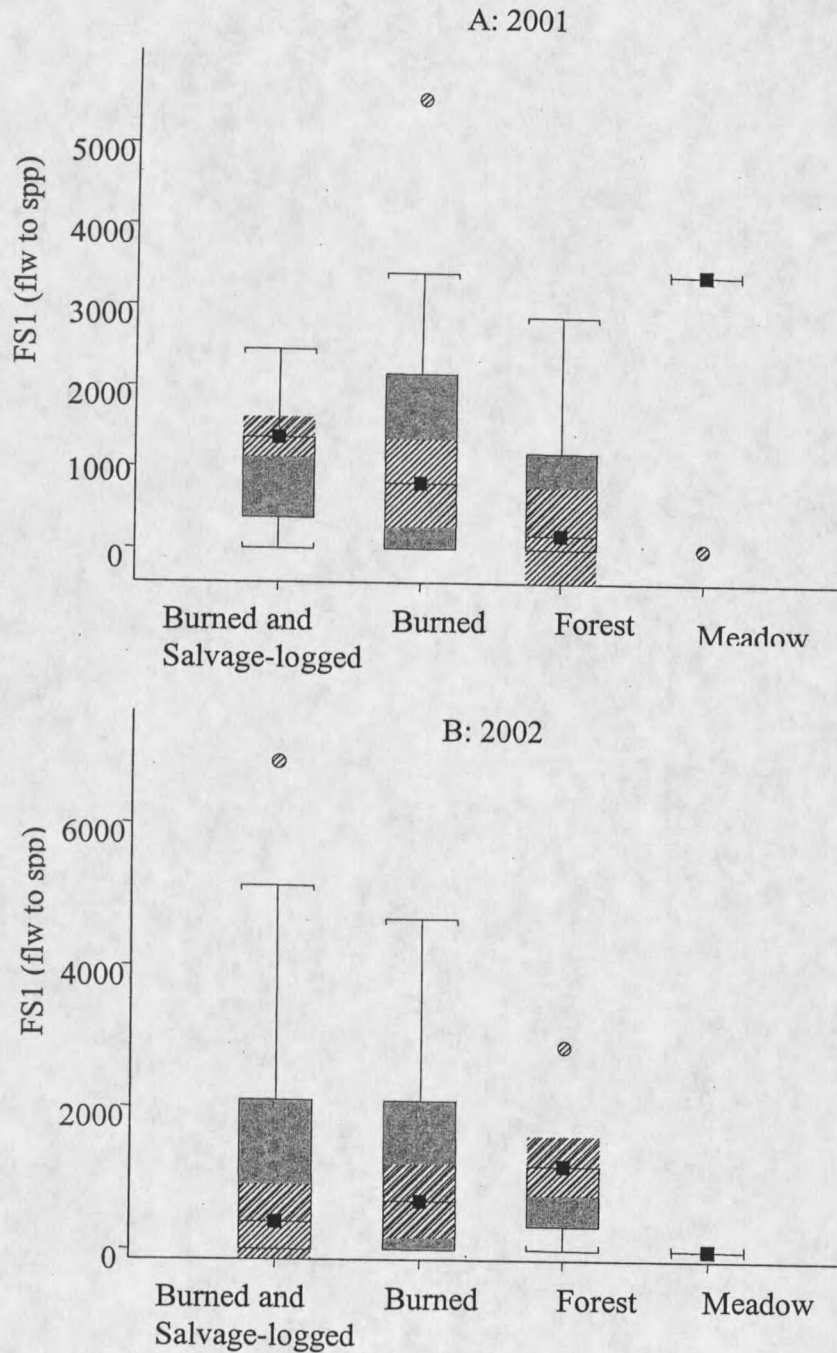


Figure 24. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

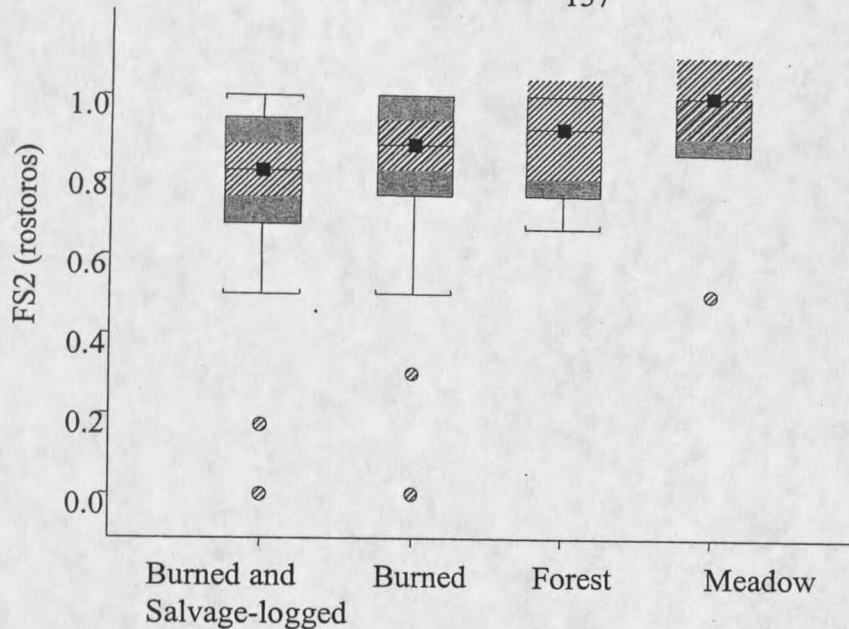


Figure 25. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

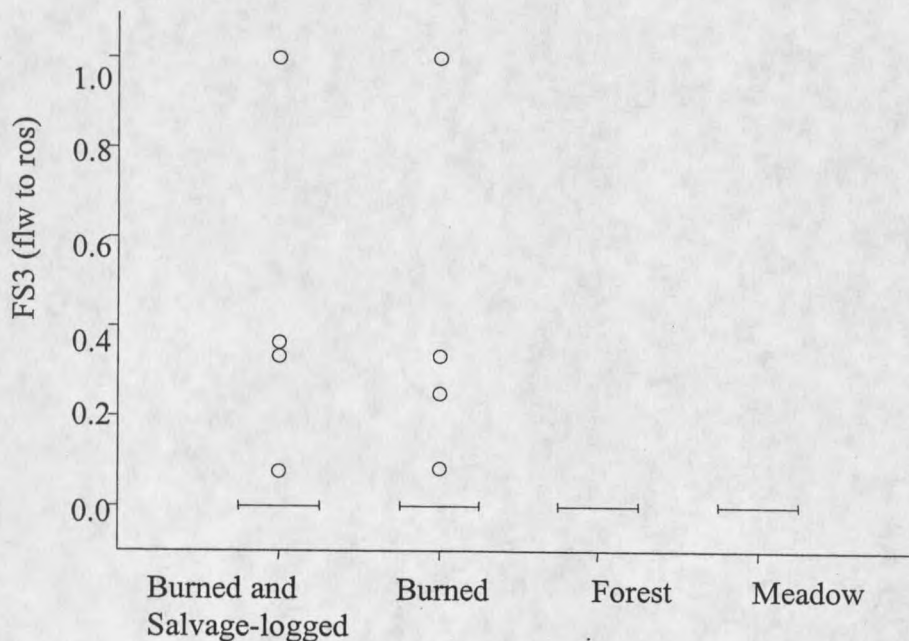


Figure 26. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

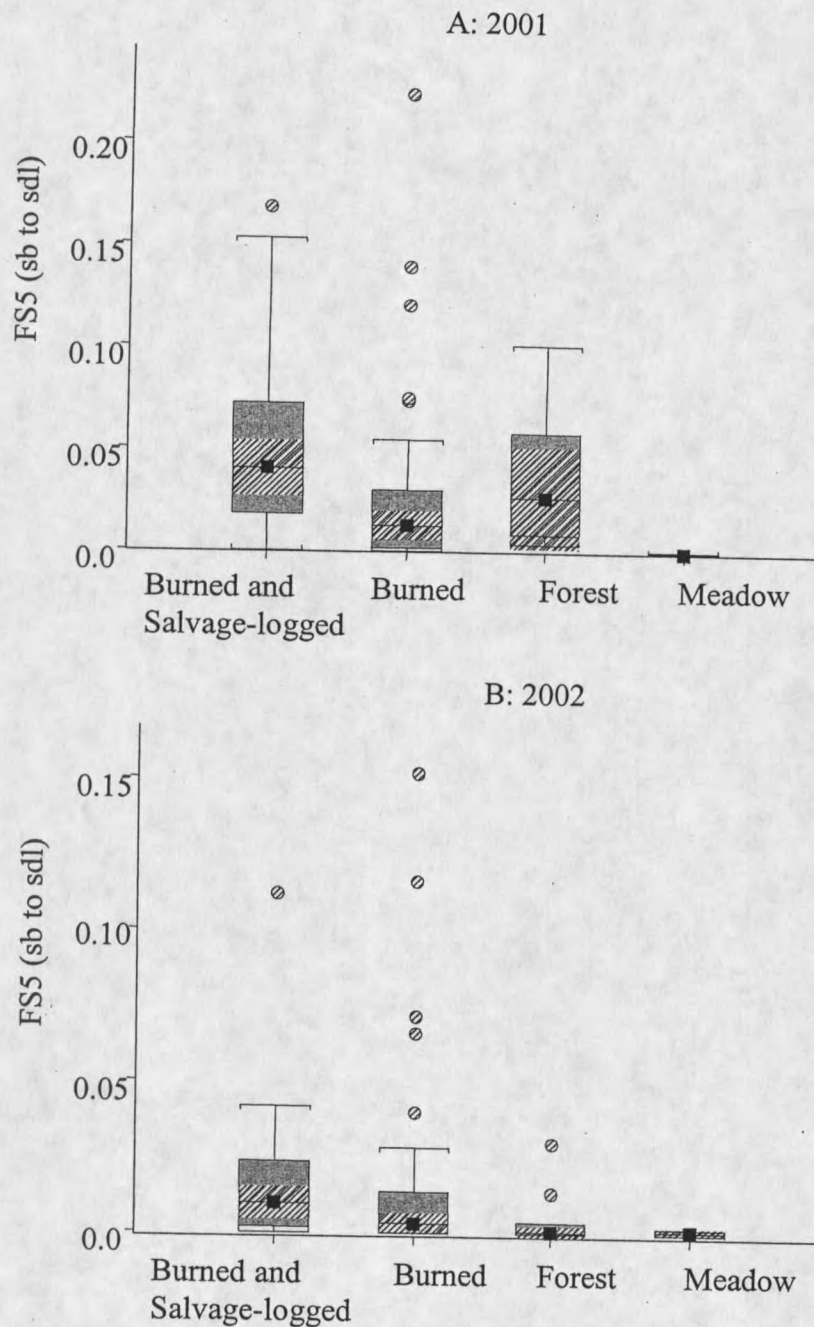
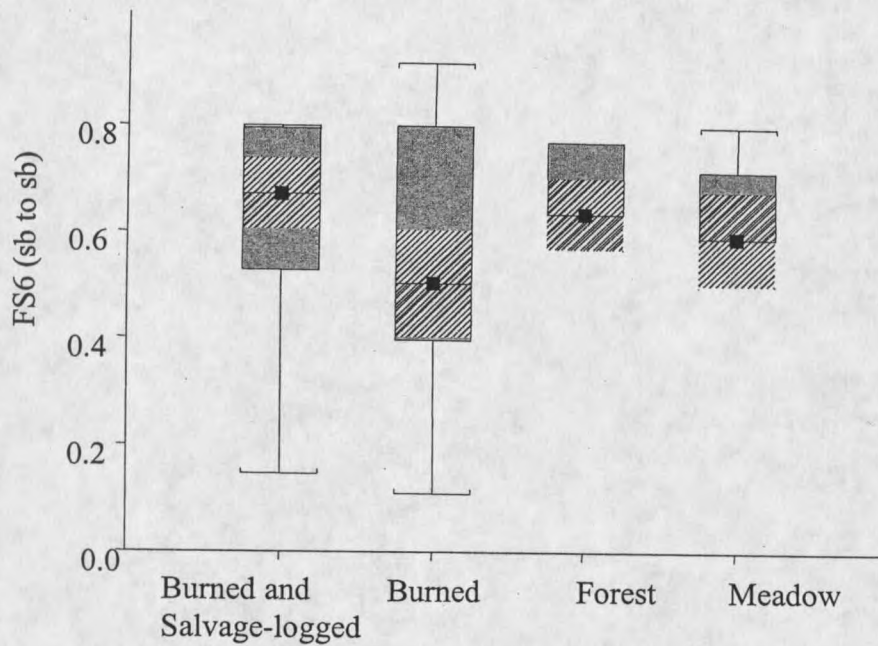


Figure 27. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

A: 2001



B: 2002

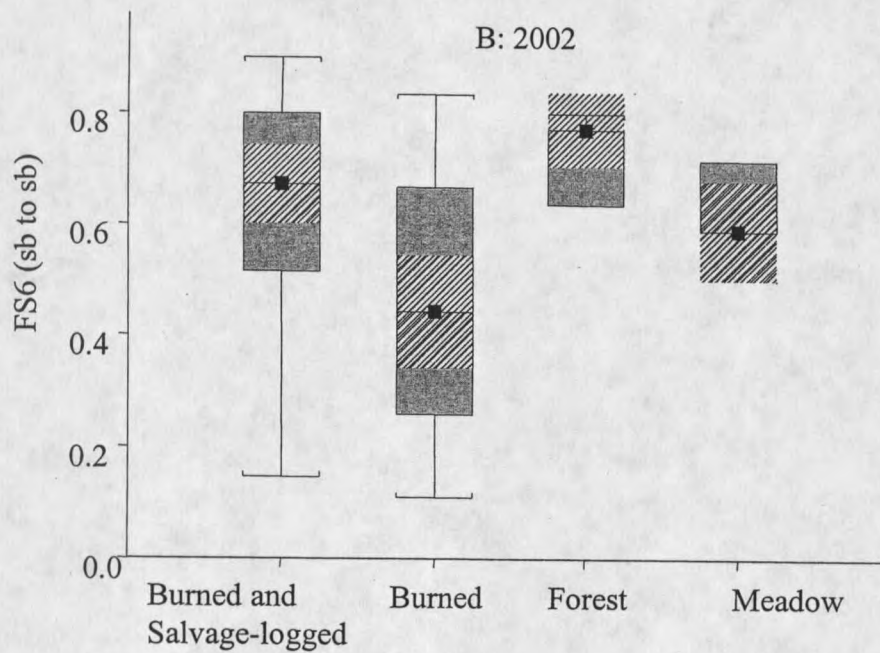


Figure 28. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

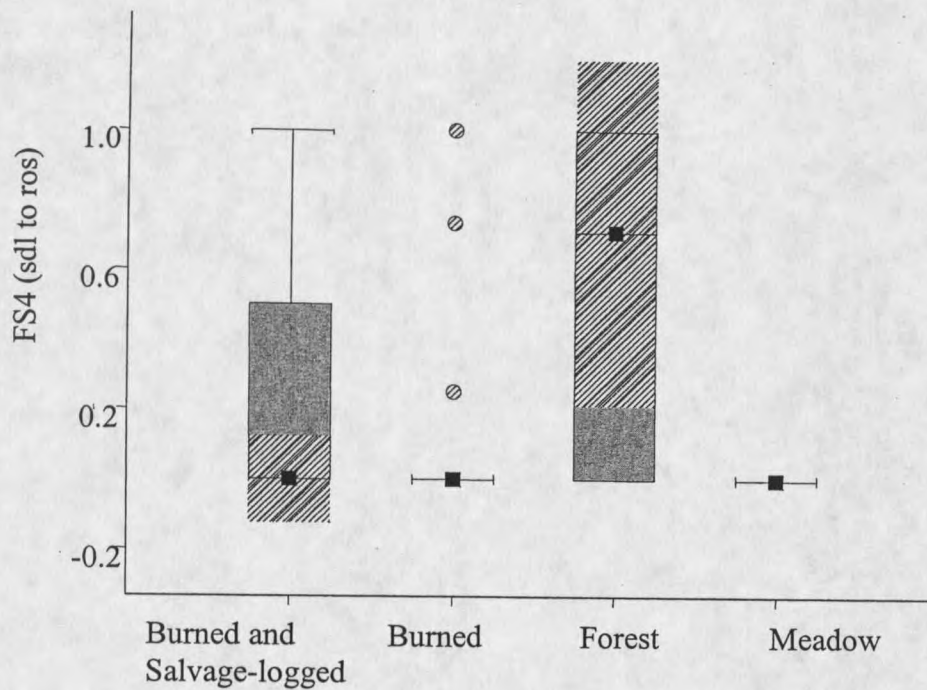


Figure 29. Median seedling to rosette transition rates from spring to fall for 2001 (A) and 2002 (B). Shown are the median (central line and box), 50% of data (light shaded box), all of data (whiskers) except for outliers (circles), and 95 % confidence interval for the median (dark shaded, hatched box) across environments.

APPENDIX B

DENSITY DEPENDENCE ANALYSIS

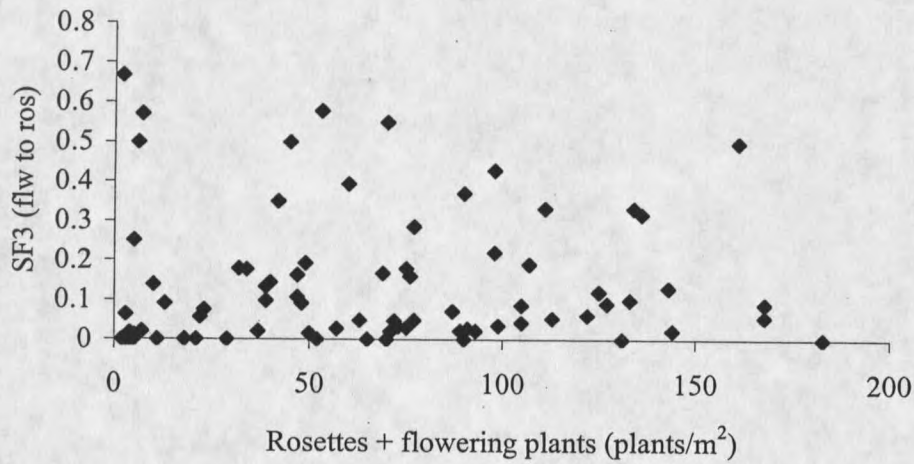


Figure 30. Relationship between tansy ragwort mature plant density and vegetative reproduction (SF3) in the Burned and Salvage-logged environment for 2001 and 2002.

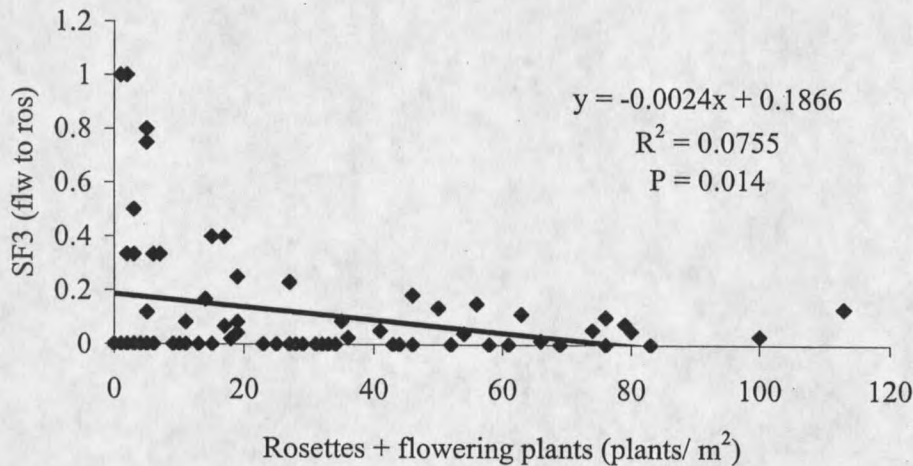


Figure 31. Relationship between tansy ragwort mature plant density and vegetative reproduction (SF3) in the Burned environment for 2001 and 2002.

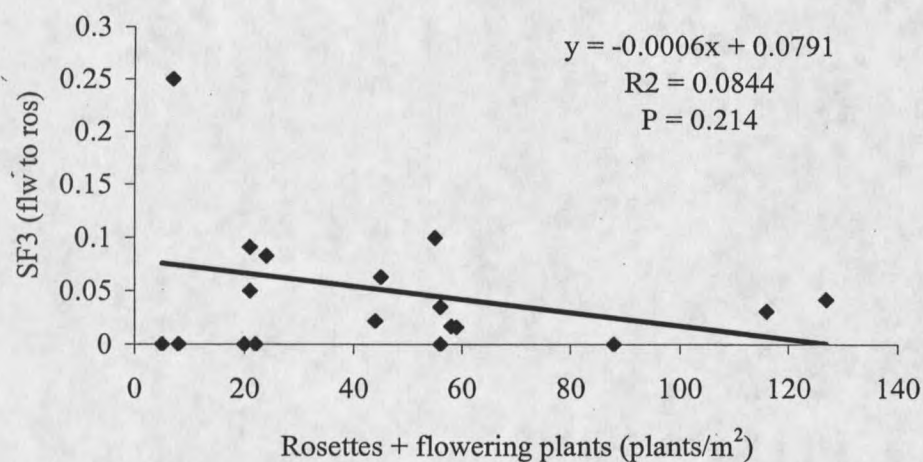


Figure 32. . Relationship between tansy ragwort mature plant density and vegetative reproduction (SF3) in the Forest environment for 2001 and 2002.

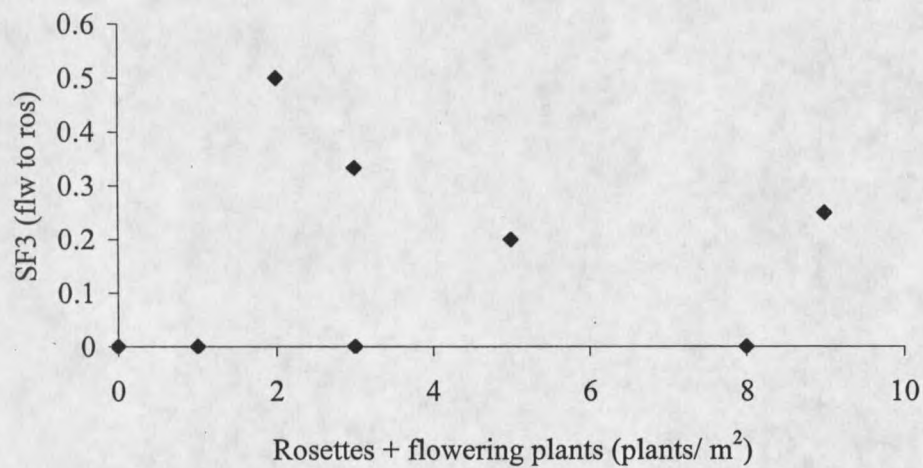
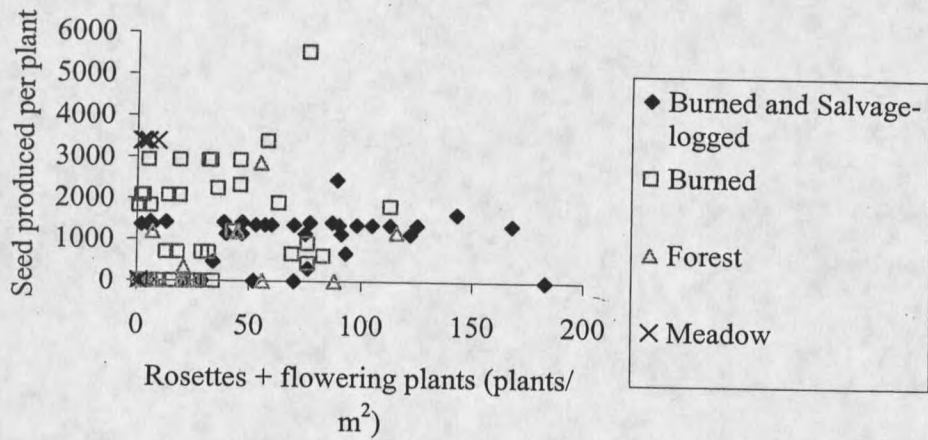


Figure 33. Relationship between tansy ragwort mature plant density and vegetative reproduction (SF3) in the Meadow environment for 2001 and 2002.

A: 2001



B: 2002

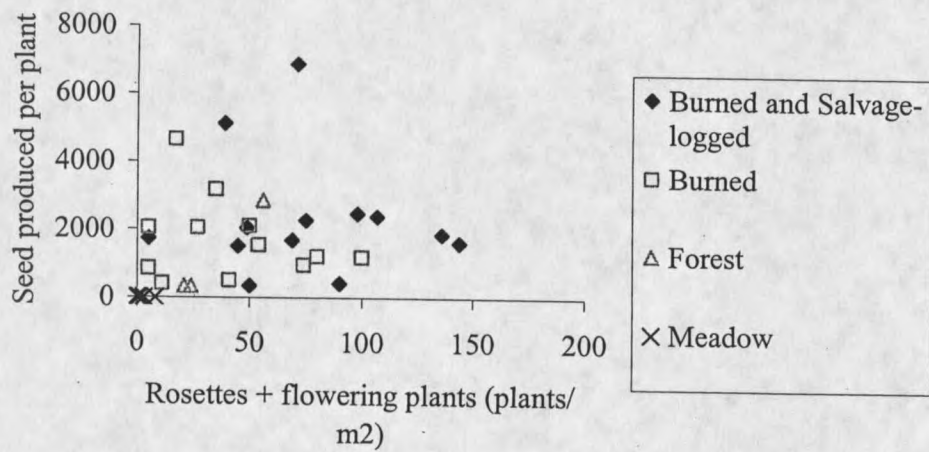
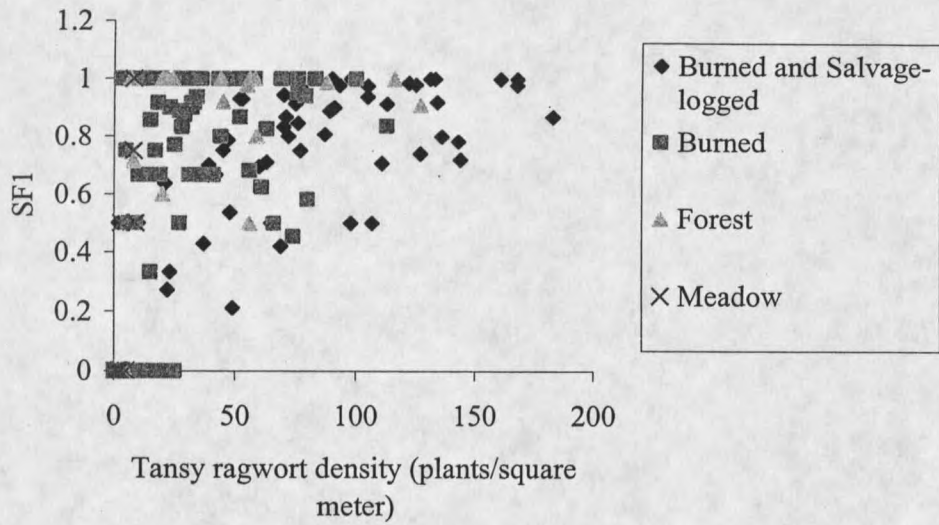


Figure 34. Relationship between tansy ragwort mature plant density and seed produced per plant in each of the four different environments in 2001 (A) and 2002 (B).

A: SF1



B: SF2

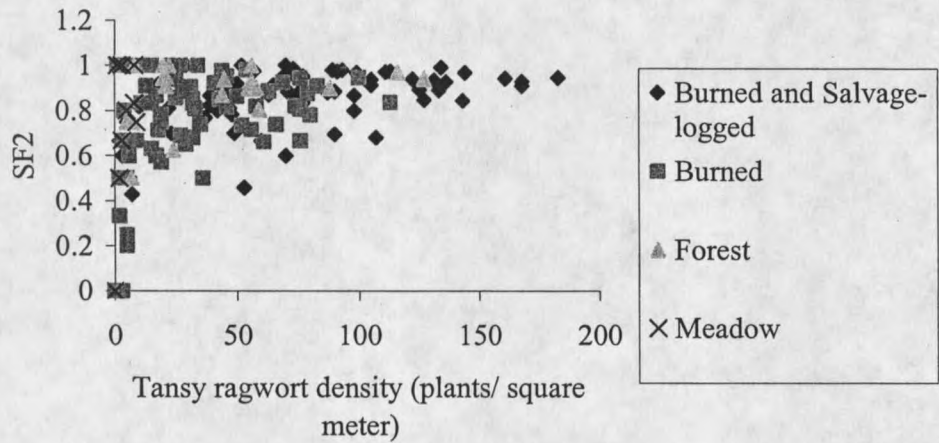
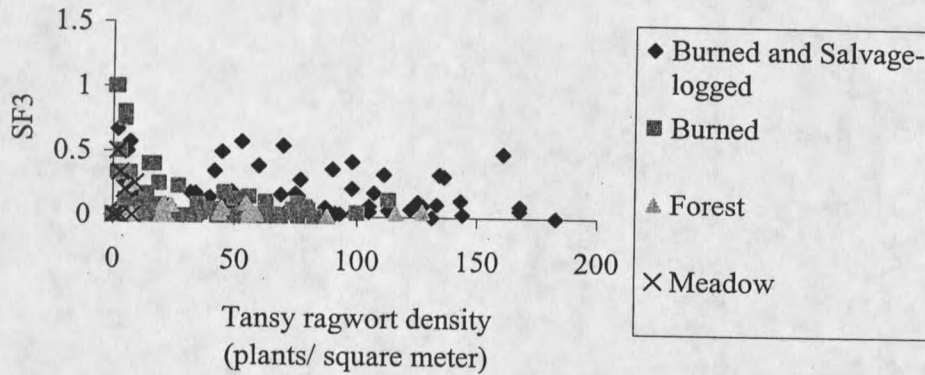


Figure 35. Relationship between tansy ragwort mature plant density and SF1 (A) and SF2 (B) in each of the four environments for 2001 and 2002.

A: SF3



B: SF4

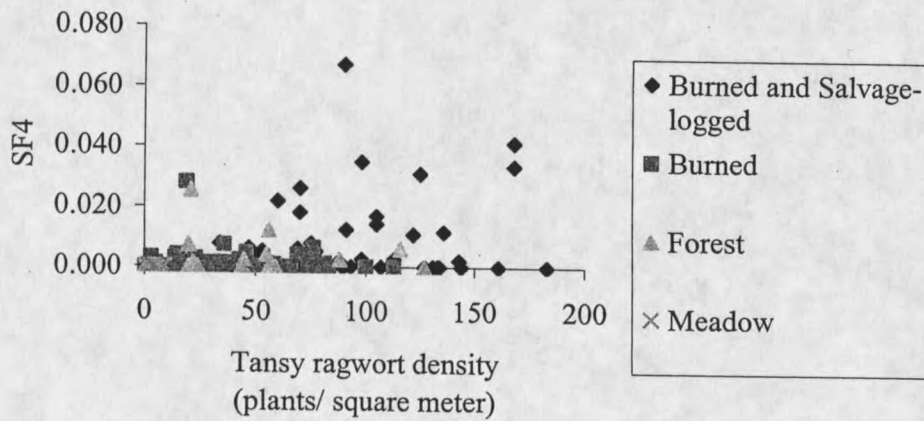


Figure 36. Relationship between tansy ragwort mature plant density and SF3 (A) and SF4 (B) in each of the four environments for 2001 and 2002.

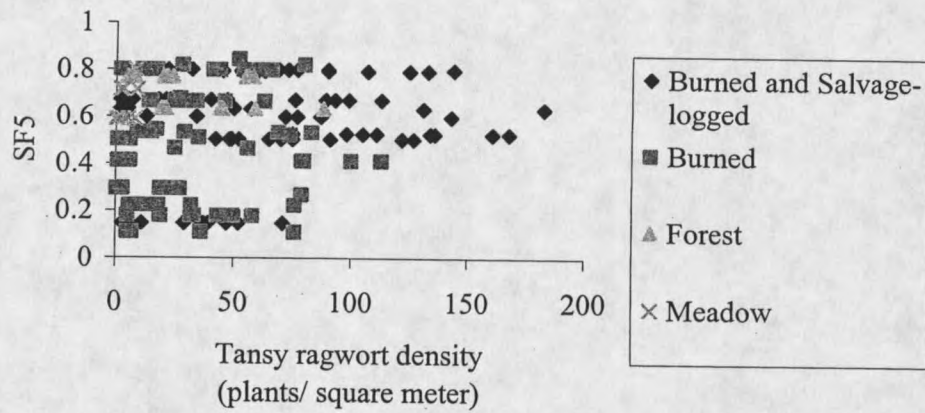


Figure 37. Relationship between tansy ragwort mature plant density and SF3 (A) and SF4 (B) in each of the four environments for 2001 and 2002.

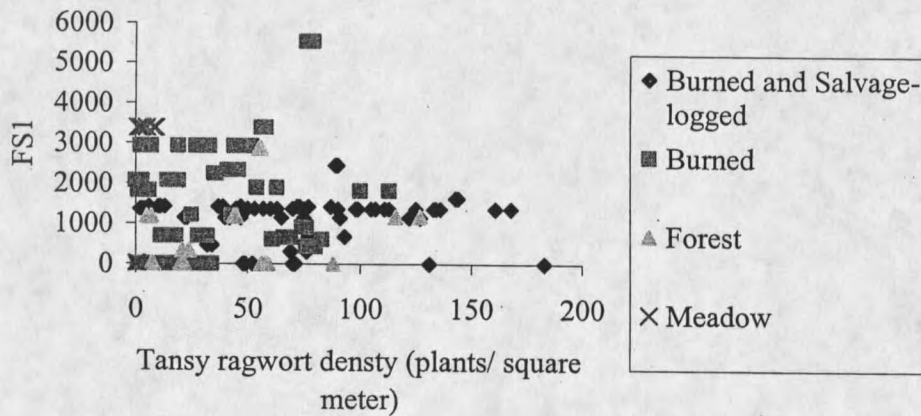
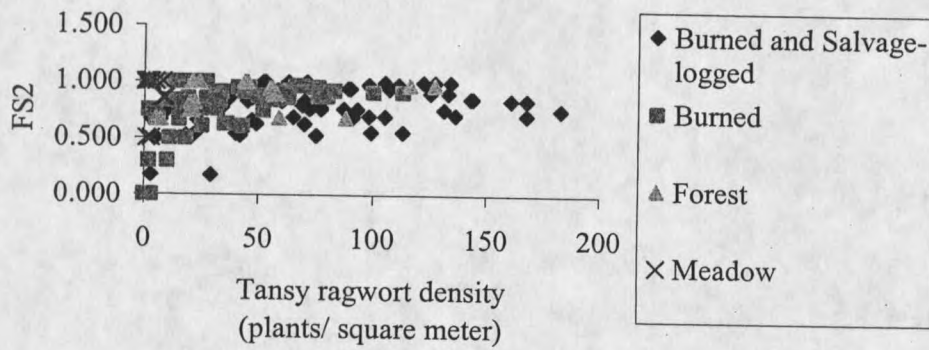


Figure 38. Relationship between tansy ragwort mature plant density and FS1 in each of the four environments for 2001 and 2002.

A: FS2



B: FS3

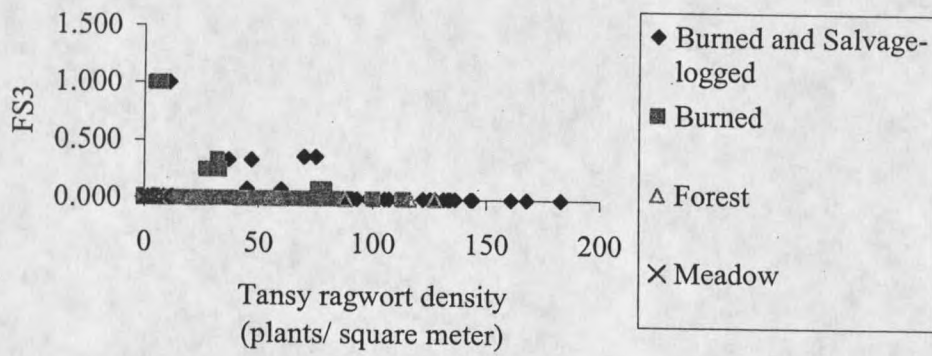
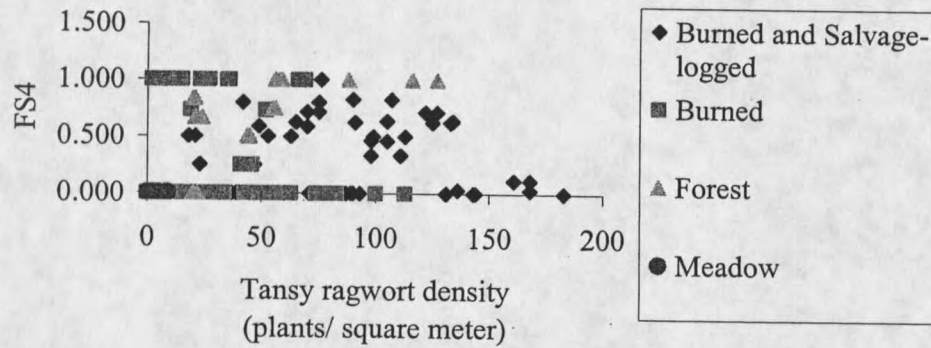


Figure 39. Relationship between tansy ragwort mature plant density and FS2 (A), FS3 (B) in each of the four environments for 2001 and 2002.

A: FS4



B: FS5

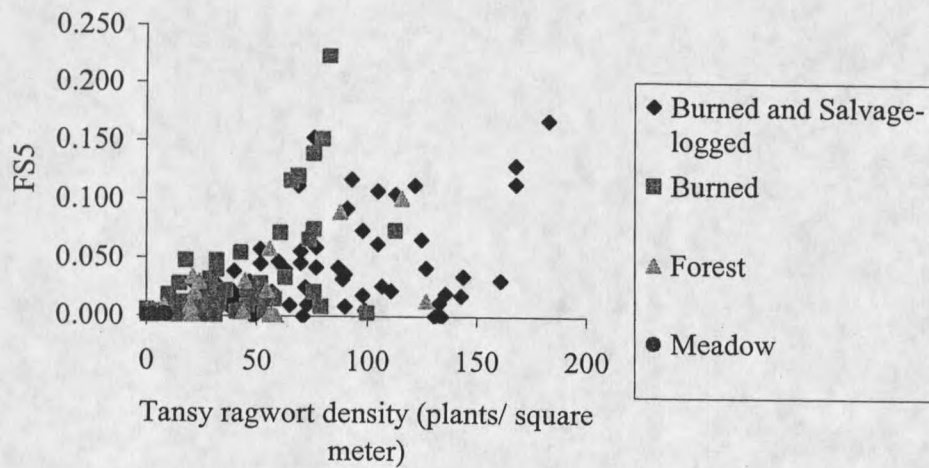


Figure 40. Relationship between tansy ragwort mature plant density and FS4 (A) and FS5 (B) in each of the four environments for 2001 and 2002.

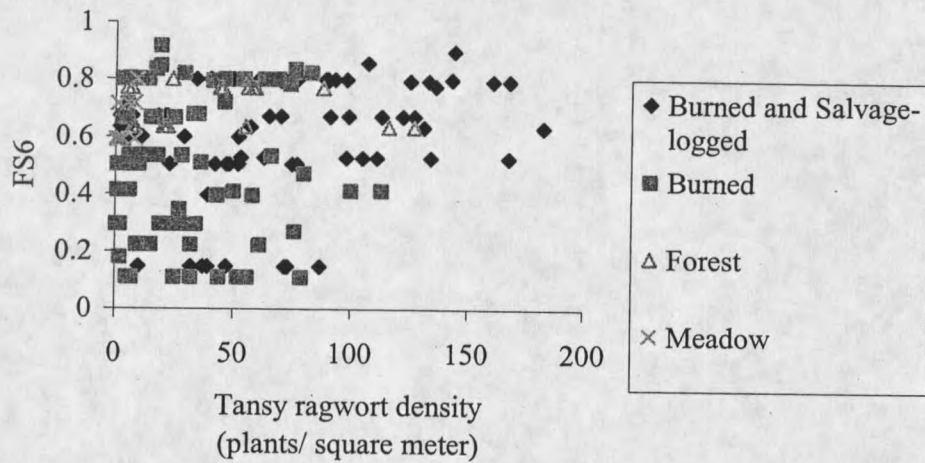


Figure 41. Relationship between tansy ragwort mature plant density and FS6 in each of the four environments for 2001 and 2002.

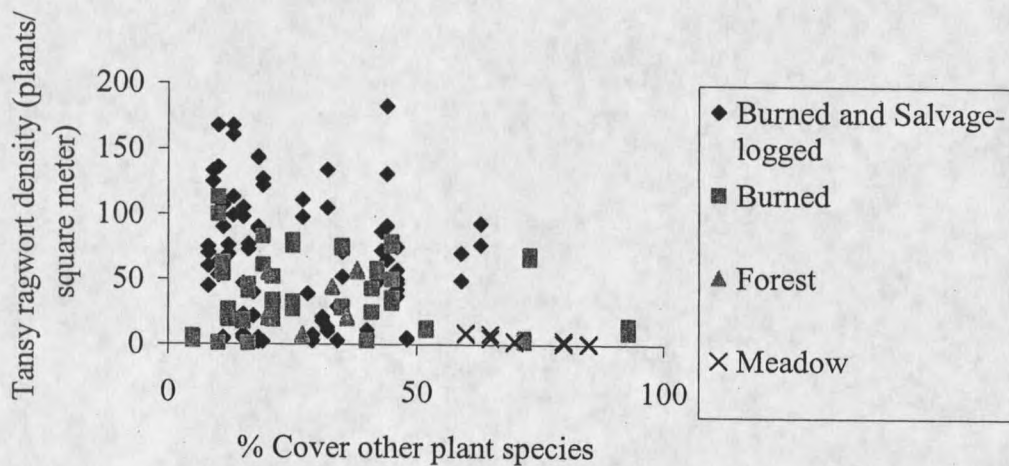


Figure 42. Relationship between percent cover of other plant species and tansy ragwort mature plant density in each of the four environments for 2001 and 2002.

APPENDIX C

SOIL CHARACTERISTIC ANALYSIS

A: Meadow

	Total N	FS2	%OM	Olsen-ba	K ppm	Mg ppm	Ca ppm	pH
FS2	-0.919 0.027							
%OM	0.996 0.000	-0.947 0.015						
Olsen-ba	0.058 0.927	0.239 0.699	-0.005 0.994					
K ppm	0.770 0.128	-0.540 0.348	0.746 0.148	0.511 0.378				
Mg ppm	0.838 0.077	-0.865 0.058	0.869 0.056	-0.300 0.624	0.660 0.226			
Ca ppm	0.904 0.035	-0.897 0.039	0.925 0.024	-0.256 0.678	0.680 0.207	0.985 0.002		
pH	-0.453 0.443	0.299 0.625	-0.401 0.503	-0.185 0.766	-0.105 0.866	0.020 0.975	-0.150 0.810	
CEC	0.991 0.001	-0.961 0.009	0.996 0.000	-0.037 0.953	0.695 0.193	0.847 0.070	0.908 0.033	-0.439 0.459

B: Burned and Salvage-logged

	Total N	FS2	% OM	Olsen P	K ppm	Mg ppm	Ca ppm	pH
FS2	0.229 0.154							
% OM	0.875 0.000	0.174 0.282						
Olsen P	-0.238 0.139	-0.367 0.020	-0.318 0.046					
K ppm	0.292 0.068	-0.129 0.429	0.049 0.764	0.214 0.185				
Mg ppm	0.673 0.000	0.234 0.146	0.521 0.001	-0.443 0.004	0.348 0.028			
Ca ppm	0.604 0.000	0.178 0.271	0.534 0.000	-0.325 0.041	0.579 0.000	0.675 0.000		
pH	-0.048 0.768	0.048 0.769	-0.058 0.724	-0.099 0.544	0.410 0.009	0.152 0.350	0.588 0.000	
CEC	0.807 0.000	0.177 0.275	0.701 0.000	-0.274 0.088	0.513 0.001	0.665 0.000	0.805 0.000	0.098 0.548

Cell Contents: Pearson correlation
P-Value

Figure. 43. Pearson correlation matrix for selected soil characteristics and FS2 in the Meadow (A) and the Burned and Salvage-logged environments (B).

A: Burned

	Total N	FS2	% OM	Olsen-ba	K ppm	Mg ppm	Ca ppm	pH
FS2	-0.089 0.639							
% OM	0.527 0.003	0.005 0.981						
Olsen-ba	-0.326 0.079	0.163 0.389	-0.131 0.491					
K ppm	0.051 0.788	-0.206 0.276	-0.115 0.545	0.192 0.309				
Mg ppm	0.552 0.002	-0.010 0.959	0.170 0.370	-0.512 0.004	-0.152 0.421			
Ca ppm	0.545 0.002	-0.342 0.064	0.218 0.248	0.050 0.793	0.538 0.002	0.307 0.099		
pH	-0.336 0.070	-0.173 0.362	-0.392 0.032	0.405 0.026	0.611 0.000	-0.234 0.213	0.451 0.012	
CEC	0.828 0.000	-0.203 0.281	0.644 0.000	-0.236 0.209	0.199 0.292	0.522 0.003	0.782 0.000	-0.131 0.489

B: Forest

	Total N	FS2	%OM	Olsen-ba	K ppm	Mg ppm	Ca ppm	pH
FS2	0.502 0.140							
%OM	0.979 0.000	0.461 0.180						
Olsen-ba	0.625 0.054	0.158 0.662	0.675 0.032					
K ppm	0.635 0.049	0.265 0.460	0.581 0.078	0.695 0.026				
Mg ppm	0.499 0.142	0.243 0.498	0.523 0.121	0.276 0.440	0.608 0.062			
Ca ppm	0.642 0.045	0.247 0.492	0.613 0.059	-0.004 0.992	0.237 0.510	0.630 0.051		
pH	-0.343 0.332	-0.102 0.778	-0.483 0.157	-0.498 0.143	-0.156 0.668	-0.162 0.655	0.129 0.722	
CEC	0.795 0.006	0.271 0.449	0.818 0.004	0.280 0.434	0.430 0.215	0.736 0.015	0.885 0.001	-0.309 0.385

Cell Contents: Pearson correlation
P-Value

Figure 44. Pearson correlation matrix for selected soil characteristics and FS2 in the Burned (A) and the Forest environments (B).

APPENDIX D

MACROS FOR TRANSITION MATRIX MODEL

```
Sub MonteCarlo()
```

```
' MonteCarlo Macro
```

```
' Macro recorded 7/29/2002 by bmax
```

```
' Keyboard Shortcut: Ctrl+m
```

```
' Make sure that you change the Sheet name when you  
' are doing simulations from different Sheets.
```

```
Sheets("Simulation-3").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 = 1 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)
```

```
If rep >= 1 And rep < Int(repn * 0.25) Then
```

```
  Do Until plot >= 5 And plot <= 24
```

```
    plot = Int(24 * Rnd) ' Generate random value between 5 and 24
```

```
  Loop
```

```
  ElseIf rep >= Int(repn * 0.25) And rep < Int(repn * 0.5) Then
```

```

Do Until plot >= 25 And plot <= 44
    plot = Int(44 * Rnd) ' Generate random value between 25 and 44
Loop
ElseIf rep >= Int(repn * 0.5) And rep < Int(repn * 0.75) Then
    Do Until plot >= 45 And plot <= 64
        plot = Int(64 * Rnd) 'Generate random value between 45 and 64
    Loop
ElseIf rep >= Int(repn * 0.75) And rep <= repn Then
    Do Until plot >= 65 And plot <= 84
        plot = Int(84 * Rnd) 'Generate random value between 65 and 84
    Loop
End If

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)
    If rep >= 1 And rep < Int(repn * 0.25) Then
        Do Until plot >= 85 And plot <= 104
            plot = Int(104 * Rnd) ' Generate random value between 85 and 104
        Loop
    ElseIf rep >= Int(repn * 0.25) And rep < Int(repn * 0.5) Then
        Do Until plot >= 105 And plot <= 124
            plot = Int(124 * Rnd) ' Generate random value between 105 and 124
        Loop
    ElseIf rep >= Int(repn * 0.5) And rep < Int(repn * 0.75) Then
        Do Until plot >= 125 And plot <= 144
            plot = Int(144 * Rnd) ' Generate random value between 125 and 144
        Loop
    ElseIf rep >= Int(repn * 0.75) And rep <= repn Then
        Do Until plot >= 145 And plot <= 164
            plot = Int(164 * Rnd) ' Generate random value between 145 and 164
        Loop
    End If

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)

```

```

Do Until plot >= 165 And plot <= 184
  plot = Int(184 * Rnd) ' Generate random value between 165 and 184
Loop
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)
  Do Until plot >= 185 And plot <= 194
    plot = Int(194 * Rnd) ' Generate random value between 185 and 194
  Loop
End If
'Get transition values for fall to spring transitions
sdltoSDLfs = 0
rostoROSLfs = 0
flwtoFLWfs = 0
sptoSPfs = 0
sbtoSBfs = Cells(plot, 13)
sdltoROSfs = Cells(plot, 12)
rostoROfs = Cells(plot, 10)
flwtoROfs = Cells(plot, 11)
sptoroSPfs = 0
sbtoroSBfs = 0
sdltoFLWfs = 0
rostoFLWfs = 0
flwtoFLWfs = 0
sptoFLWfs = 0
sbtoFLWfs = 0
sdltoSPfs = 0
rostoSPfs = 0
flwtoSPfs = Cells(plot, 9)
sptoSPfs = 0
sbtoSPfs = 0
sdltoSBfs = 0
rostoSBfs = 0
flwtoSBfs = 0
sptoSBfs = 0
sbtoSBfs = Cells(plot, 8)

'Get transition values for spring to fall transitions
sdltoSDLsf = 0
rostoROSLsf = 0
flwtoFLWsf = 0

```

```

sptosdlf = 0
sbtosdlf = Cells(plot, 6)
sdltorossf = Cells(plot, 3)
rostorossf = Cells(plot, 4)
flwtorossf = 0
sptorossf = 0
sbtorossf = 0
sdltoflwsf = 0
rostoflwsf = Cells(plot, 5)
flwtoflwsf = 0
sptoflwsf = 0
sbtoflwsf = 0
sdltofpsf = 0
rostofpsf = 0
flwtofpsf = 0
sptofpsf = 0
sbtofpsf = 0
sdltofbfs = 0
rostofbfs = 0
flwtofbfs = 0
sptofbfs = 1#
sbtofbfs = Cells(plot, 7)

ngen = Cells(3, 22)
For t = 1 To ngen
    pop0 = ROSf + FLWf
    'Fall to spring transitions
    SDLs = SDLf * sdtosdlf + ROSf * rostosdlf + FLWf * flwtosdlf + SPf * sptosdlf
+ SBf * sbtosdlf
    ROSs = SDLf * sdtorosf + ROSf * rostorosf + FLWf * flwtorosf + SPf *
sptorosf + SBf * sbtorosf
    FLWs = SDLf * sdtoflwf + ROSf * rostoflwf + FLWf * flwtoflwf + SPf *
sptoflwf + SBf * sbtoflwf
    SPs = SDLf * sdtospf + ROSf * rostospf + FLWf * flwtospf + SPf * sptospf +
SBf * sbtospf
    SBs = SDLf * sdtosbfs + ROSf * rostosbfs + FLWf * flwtosbfs + SPf * sptosbfs +
SBf * sbtosbfs

    'Spring to fall transitions
    SDLf = SDLs * sdtosdlf + ROSs * rostosdlf + FLWs * flwtosdlf + SPs *
sptosdlf + SBs * sbtosdlf
    ROSf = SDLs * sdltorossf + ROSs * rostorossf + FLWs * flwtorossf + SPs *
sptorossf + SBs * sbtorossf
    FLWf = SDLs * sdltoflwsf + ROSs * rostoflwsf + FLWs * flwtoflwsf + SPs *
sptoflwsf + SBs * sbtoflwsf

```

SPf = SDLs * sdtospsf + ROSs * rostospsf + FLWs * flwtospsf + SPs * sptospsf + SBs * sbtospsf

SBf = SDLs * sdtosbsf + 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 = 1 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 E

CONVERSION POLYNOMIAL FORMULA FOR K-TYPE THERMOCOUPLES

Conversion polynomial formula for K-type thermocouple:

Thermister conversion:

$$(\text{bit value} / 4) * 0.15 - 23.65$$

Temperature conversion:

$$(25.132785 * (\text{cold junction value} / 4 / 24)) - (((6.0883423 * 10^{-5}) * (\text{cold junction value} / 4 / 24))^2) + (((5.5358209 * 10^{-10}) * ((\text{cold junction value} / 4 / 24))^3) + (((9.3720918 * 10^{-15}) * ((\text{cold junction value} / 4 / 24))^4)) + \text{thermister conversion value}$$

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