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Age structure and age-related performance of sulfur cinquefoil (*Potentilla recta*)

Dana L. Perkins
Bureau of Land Management, Challis Field Office, Challis, ID 83226

Catherine G. Parks
Corresponding author. USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850; cparks01@fs.fed.us

Kathleen A. Dwire
USDA Forest Service, Rocky Mountain Research Station, Laramie, WY 82070

Bryan A. Endress
Forest Science Department, Oregon State University, Corvallis, OR 97331

Kelsi L. Johnson
(formerly) USDA Forest Service, Pacific Northwest Research Station, LaGrande, OR 97850

Age distributions of sulfur cinquefoil populations were determined on sites that were historically grazed, cultivated, and mechanically disturbed. From 12 sites, a total of 279 reproductively active plants were collected and aged by using herbchronology (counting rings in the secondary root xylem of the root crown) to (1) estimate the age structure of the populations, (2) relate plant size and flower production to plant age, and (3) examine the relation of population age structure to environmental variables and disturbance history. Results indicated that the mean age for all sampled plants was 3.5 (± 1.74 SD) yr and ranged from 1 to 10 yr. Age was not related to number of flowers, plant size (number of stems per plant or plant height), or site disturbance type but was positively correlated with site elevation ($P < 0.001$). The pooled age distribution from all 12 sites was right-skewed with fewer old plants than young plants. We conclude that sulfur cinquefoil plants sampled in northeast Oregon are able to colonize, establish, and reproduce at disturbed sites rapidly. We suggest that herbchronology may be a useful technique to improve understanding of invasion biology and ecology for invasive plant species that form annual rings.

Nomenclature: Sulfur cinquefoil, *Potentilla recta* L. PTLRC.

Key words: Age determination, age distribution, demography, herbaceous perennials, population biology.

The nonnative, invasive plant, sulfur cinquefoil (*Potentilla recta* L.), has been recognized as having broad ecological amplitude in the semiarid climates of Idaho, Montana, eastern Oregon and Washington, and British Columbia (Rice 1991, 1999; Rice et al. 1999). It forms dense and continuous populations, most commonly on areas of soil disturbance and is considered a threat to native plant communities. Increasingly, sulfur cinquefoil populations have been observed in native-species–dominated rangelands and in the understory of open-canopied ponderosa pine forests (Naylor et al. 2005).

Often, insufficient information is known about the basic biology and population development of an invasive species to launch efficient control and management programs (Hobbs and Humphries 1995). Through increased understanding of the demography (growth, survival, and reproduction) of invasive plants, it may be possible to predict the behavior of populations in a particular area, to identify crucial stages of the life cycle that contribute to population growth, and to target those stages as part of a management strategy. Therefore, studying the demography and population ecology of invasive species is an important step toward managing plant invasions (e.g., Buckley et al. 2003a, 2003b; Paynter et al. 2003).

The age structure of a population can be used to characterize the demography of plant populations (Harper 1977). Age provides a timeline needed for assessing population dynamics and patterns of persistence of species. Stable populations often have a reversed J-Shape age distribution (Ågren and Eriksson 1990; Leak 1965), and age is frequently related to growth, survival and reproductive potential of species. Determining the age structure of invasive plant populations has been used to provide insights on invasive plant life histories, patterns of colonization, and spread for several woody species (Deering and Vankat 1999; Paynter et al. 2003; Webb et al. 2000).

Until recently, determining age structures of forb species was difficult and was estimated by either morphological features (Kuen and Erschbamer 2002) or by following individuals over time (Inghe and Tamm 1985). More often, age was deemed not determinable. Recently, studies from temperate regions in Europe and North America have shown that many herbaceous perennials exhibit annual rings in the secondary xylem of their roots (Dietz and Ullman 1997, 1998; Schweingruber and Dietz 2001; Dietz and Schweingruber 2002). The method of age determination by counting growth rings in the roots of herbaceous perennials has been called "herbchronology" (Dietz and Ullman 1997, 1998). Herbchronology allows researchers to address questions that had previously been difficult or impossible to study. For example, recent applications of herbchronology include evaluation of relations of plant age and morphology, documentation of colonization patterns of disturbed sites, age structure as related to environmental gradients, and the use of age structure to infer population growth rates (Dietz and Ullman 1998). Therefore, herbchronology may be a useful tool for examining the invasion biology of nonnative invasive forbs. In invasive plant research, herbchronology has been used in a number of studies to evaluate species spread rates (Boggs and Story 1987; Dietz 2002) and age-disturbance relationships (Dietz and Ullman 1998). Sulfur cinquefoil was first noted as having annual rings by Werner and Soule (1976) and more recently verified with plants of known ages (Dietz and Ullman 1997).

In this article, we assess the use of herbchronology in determining age-structures of populations of the invasive

TABLE 1. Physical site attributes and disturbance classes for the 12 sulfur cinquefoil populations. Elevation has been divided into classes based on 200-m intervals.

Site	Disturbance class	Elevation (m)	Elevation class	Aspect	Slope (degrees)
HH	grazed	860	low	E	6
FHE	cultivated	830	low	E	6
FHW	grazed	850	low	E	9
LG	mechanical	730	low	S	18
RB	mechanical	970	moderate	NW	3
SH	cultivated	950	moderate	S	7
GLS	mechanical	910	moderate	SW	3
DALE	cultivated	900	moderate	E	8
ML	mechanical	1,285	high	N	6
RICE	mechanical	1,225	high	W	15
SC	mechanical	1,165	high	SE	4
CC	mechanical	1,360	high	NW	9

plant, sulfur cinquefoil, in northeastern Oregon and examine the relationships between (1) age and plant size and reproduction, (2) age and physical site attributes, and (3) age structure and human-related disturbance.

Materials and Methods

Study Area

The study area was located in the Blue Mountains of northeastern Oregon in a transition area between maritime and continental climates. Average annual precipitation reported from La Grande, OR, the closest meteorological station to the study area, is 43 cm (1965 to 2003 average) (Western Regional Climate Center, Reno, NV). Most precipitation occurs from October through May, with drier summer months characterized by periodic thunderstorms. Average temperatures during 1965 to 2003 ranged from 3 C to 16 C. The study sites spanned a 13,000 km^2 area, were located over a range of elevations and slopes, and were selected to complement a separate study on sulfur cinquefoil seed production and dispersal at these sites (Dwire et al. in press). Sites ranged in their physical attributes (slope, elevation, aspect) and disturbance histories (Table 1). All sites were located on areas that are or once were dominated by perennial bunchgrass species, such as bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*), with little to no tree canopy cover. Each study location was extensively infested with sulfur cinquefoil with densities reaching up to 150 stems m^{-2} (B. A. Endress, unpublished data). Soils in the study region are variable, but most are derived from volcanic materials including volcanic debris and ash, andesite, basalts, rhyolites, and tuffs (Bryce and Omernik 1997). All study sites were located within 500 m of roads, were impacted by human-related disturbances, and were grazed by native wildlife, primarily elk and deer. Disturbance from land use activities was categorized into three types: (1) mechanical soil disturbance, (2) cultivation, and (3) livestock grazing (Table 1). Mechanical soil disturbance refers to past and ongoing soil disturbance by mechanized equipment associated with railroads, roads, developed recreation, and power lines. Mechanical soil disturbance sites have chronic vehicle traffic and are disturbed by human-related maintenance activities such as soil deposition and removal. Cultivation disturbance refers to previous agricultural tilling (i.e., old fields); cultivated sites were plowed in the past and have been fallow for at least 5 yr. Grazed sites have been seasonally grazed in summer months by domestic livestock (cattle, horses, sheep) for the past 10 or more yr.

Plant Collection

Reproductively active sulfur cinquefoil plants were collected from 12 sites in northeastern Oregon from July 24 to August 24, 2001, following peak flowering. At each site, 25 or 30 plants were collected at random. Collections were restricted to adult plants that produced flowers the year of the study (2001); seedlings and nonflowering rosettes were not sampled. Plants were carefully dug from the soil with trowels and shovels to ensure that both the entire aboveground portion of the plant and the entire root network were collected intact. Plants were individually placed in plastic bags for transport. In the laboratory, the number of stems, number of flowers per stem, and plant height were recorded for each plant, and the plants were placed individually in brown paper bags to air-dry.

Aging Plants

To process the plants for aging, we first soaked the root crown in water for 24 to 48 h and then trimmed the crown to a small root segment that could be anchored in the vice of a sliding stage microtome.[1] When secured in the microtome, each root crown was sectioned at the root-shoot transition zone with a 25- by 4.5-mm stainless steel blade with a double-beveled cutting edge. The root-shoot transition zone contains the maximum number of annual rings in the secondary xylem (Roughton 1972). A 1:1 mixture of glycerine and 95% ethanol was brushed on the root cross-section before slicing to prevent the cross-section from curling or folding after slicing. Four to eight cross-sections were transferred from the microtome blade to one or more microscope slides with a small paintbrush and stained with toluidine blue O.[2] We applied a droplet of the stain to the root crown cross-sections for 1 min and then rinsed the slide with 95% ethanol for 30 to 60 s. A drop of cedar oil was then added to each slide as a mounting medium before the microscope slide cover was applied. Microscope covers were weighted and air-dried for temporary storage until annual growth rings were counted.

Microscope slides of cross-sections were viewed with a stereoscopic microscope to count annual growth rings. Ring

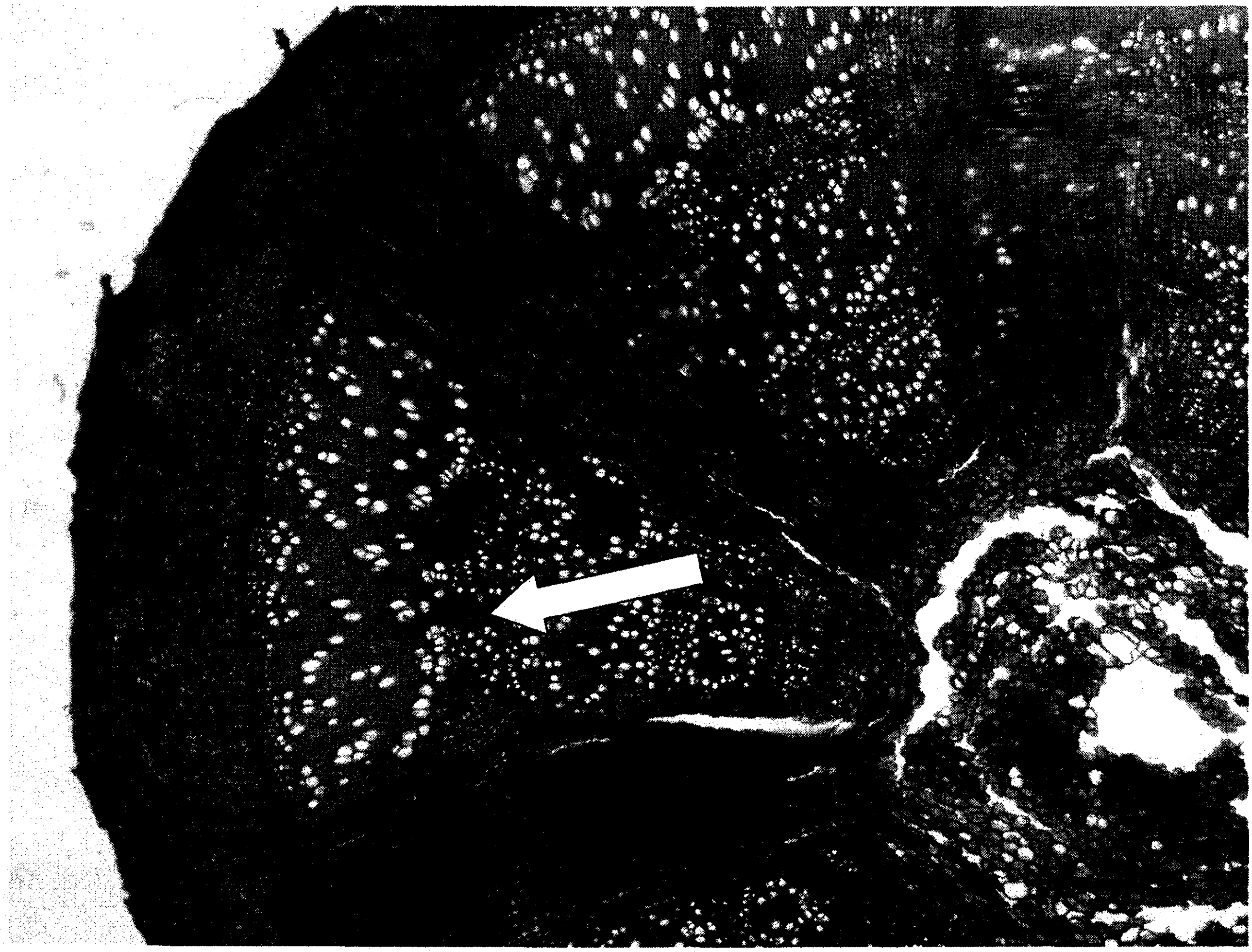

FIGURE 1. A cross-section of a sulfur cinquefoil root crown showing the semi-ring porous structure of the vessels in the growth ring and pith cells. This 4-yr-old sample was sliced with a sliding stage microtome[1]. The ring boundary (arrow) occurs between the small vessels of the previous year's latewood and the large vessels of the current year's earlywood.

structure or growth layers were identified by using methods of wood anatomy (Fahn 1974; Hoadley 1990; Schweingruber 1988). Secondary xylem was examined for the presence of early and latewood vessels in concentric rings, a differentiating characteristic for ring boundary detection (Dietz and Fattorini 2002). Two observers examined all samples, and we calculated the mean absolute difference between observations as an indicator of precision (Roughton 1972).

Data Analysis

We used exploratory data methods (Chambers et al. 1983; Tukey 1977) to characterize age patterns of the 12 sulfur cinquefoil populations both individually and collectively. Scatter plots and ordinary least-squares regressions were calculated for age versus number of flowers, number of stems, number of previous year's flowers, height, elevation, and disturbance category. To investigate the relationships of age and size and age and reproduction, we divided plants into age classes, defining young plants as those 2 to 3 yr, middle-aged plants as those 4 to 5 yr, and old plants as those 6 yr and older. One-year-old plants were not included because we may have undersampled this age class by not sampling rosette plants. We chose the three classes based on the maximum longevity of 10 yr and the relative proportions of individuals in each age class. Box plots were examined for patterns of association among age distributions, elevation classes, and disturbance classes. Inferences from our analyses are limited to the populations that we sampled. All statistical analysis was conducted with SPLUS 6.1.[3]

Results and Discussion

Herbchronology

Age-determination of sulfur cinquefoil plants by using growth rings was facilitated by visible ring boundaries in the root crown. Growth rings in the root crown were semi-ring porous (Hoadley 1990) with large vessels concentrated in the early wood, and smaller, slightly flattened or oblong vessels apparent in the late wood (Figure 1). Thus, detection of the latewood boundary was similar to the annual ring boundary in many tree species and other herbaceous perennials (Dietz and Ullman 1997, 1998; Dietz and Schweingruber 2002).

Our method of rehydrating roots and using toluidine blue

TABLE 2. Age summary statistics for sulfur cinquefoil plants sampled at 12 northeastern Oregon sites.

Site	No. collected (No. aged)	Aged (%)	Mean age ± SD	Median age (yr)	Minimum to maximum age (yr)
HH	30 (28)	97	4.0 ± 1.95	4.0	1–8
FHE	30 (23)	77	2.3 ± 0.83	2.0	1–4
FHW	30 (28)	93	3.0 ± 1.49	3.0	1–7
LG	30 (26)	80	3.2 ± 1.83	2.0	1–7
RB	30 (23)	67	2.8 ± 1.37	3.0	1–6
SH	25 (18)	72	3.2 ± 1.54	3.0	1–6
GLS	30 (20)	67	3.6 ± 1.32	4.0	1–5
DALE	30 (22)	73	3.2 ± 1.33	3.0	1–7
ML	32 (24)	75	3.9 ± 1.80	4.0	1–9
RICE	30 (27)	90	4.9 ± 2.20	4.5	2–10
SC	30 (24)	77	3.9 ± 1.24	4.0	2–7
CC	25 (22)	84	4.2 ± 1.89	4.0	1–8
Total	352 (285)	81	3.5 ± 1.74	3.0	1–10

stain in preparing cross-sections gave satisfactory results similar to other investigations that used fresh samples or samples stored in 50% alcohol before analysis. One advantage of rehydrating and processing dry plants is that lab analysis may be conducted after field season when personnel resources are more available. Additionally, others (Dietz and Ullman 1997) have used phloroglucinol/HCl, a monochromatic red stain for staining sections, and our use of toluidine blue (a polychromatic stain) stained xylem and lignin tissue a blue-green and the cortex, parenchyma, and pith cells a darker blue to blue-purple. These color contrasts helped us differentiate anatomical structures. Cross-sections of the sulfur cinquefoil root-shoot transition zone show that pith cells are found in stem tissue but absent in the root tissue (Schweingruber 1988) (Figure 1). Sulfur cinquefoil plants aged in a study in Michigan also showed clear and easily detectable ring boundaries (Dietz and Schweingruber 2002).

Age Determination and Age Distribution

We were able to age 81% of the plants collected (Table 2). Root decay and sampling-caused root crown damage were the primary reasons that we could not age all plants. Two sites, RB and GLS (Table 2), which were adjacent to streams, had the lowest percentage of datable plants and the highest degree of recorded root decomposition. Several researchers have found problems with root decomposition in mesic areas (Dietz 2002; Werner and Soule 1976). Additionally, root-feeding insect larvae present on plants from GLS reduced our effectiveness at aging individuals from that site. The precision of our age estimates was 0.034 absolute mean difference between the two observers, indicating a high degree of consistency.

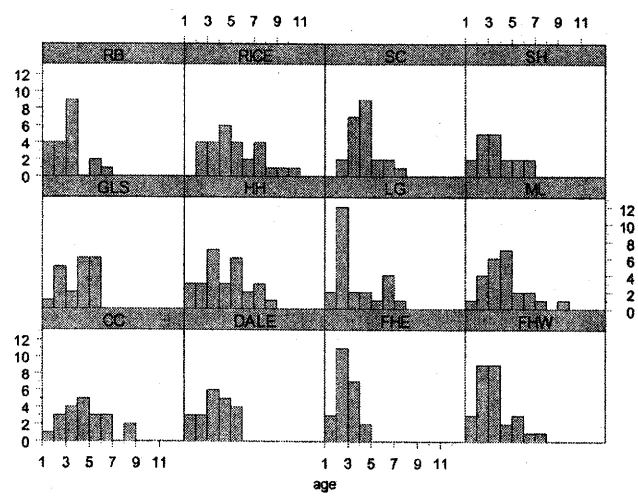

FIGURE 2. Age histograms of sulfur cinquefoil plants from 12 populations in northeastern Oregon.

Mean age for all sample plants was 3.5 (± 1.74 SD) yr, median age was 3 yr (Table 2), and plant ages ranged from 1 to 10 yr. Age distributions were continuous (i.e., no age classes absent) on seven of the sites (Figure 2). The RICE site had the oldest population with the individual representing the 10-yr-old cohort established in 1992. Thus, the longevity of sulfur cinquefoil plants at our sites in northeastern Oregon exceeds the 6 yr previously reported by Werner and Soule (1976) but is less than the 20-yr age extrapolated from the crown diameter-age relationship reported by Powell (1996). The FHE site had the youngest population; at this site the oldest cohort established in 1998 (4 yr old). Three sites, ML, CC, and RB had discontinuous distributions with one age class (1994, 1995, and 1998, or 8, 7, and 4 yr, respectively) absent. At two sites, RICE and SC, no reproductively active plants were sampled in the 1-yr age class (2001). At all sites, population age distributions were uneven aged and right skewed with fewer older plants than younger plants (Figure 2). The shapes of the distributions varied from single modal to multimodal shapes (Figure 2). Modal-shaped distributions are frequently used to infer favorable growing conditions in specific years or pulse-type recruitment events.

The age distribution from all sites collectively was also unevenly aged, and after age three, decreased monotonically (Figure 3). Fifty percent of the plants were 2 to 3 yr old, 30% were 4 to 5 yr old, and 14% were age 6 and older (Figure 3). Because we did not sample rosettes, we were unable to construct the overall population age structure for sulfur cinquefoil. If we had obtained more samples in the underrepresented age classes (1 and 2 yr olds), the distribution shape of Figure 3 may have approached a reverse-J, stable age distribution. Additional unpublished evidence supports this possibility; 400 sulfur cinquefoil plants seeded in pots and grown outdoors produced flowers in the first

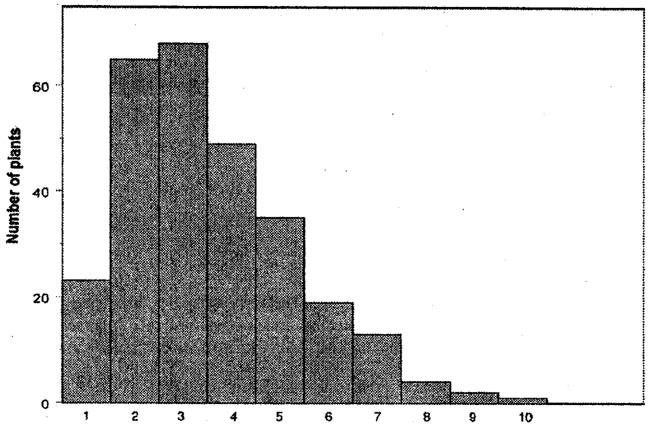

FIGURE 3. Age distributions of all sampled sulfur cinquefoil plants ages 1 and older from 12 sites in northeastern Oregon.

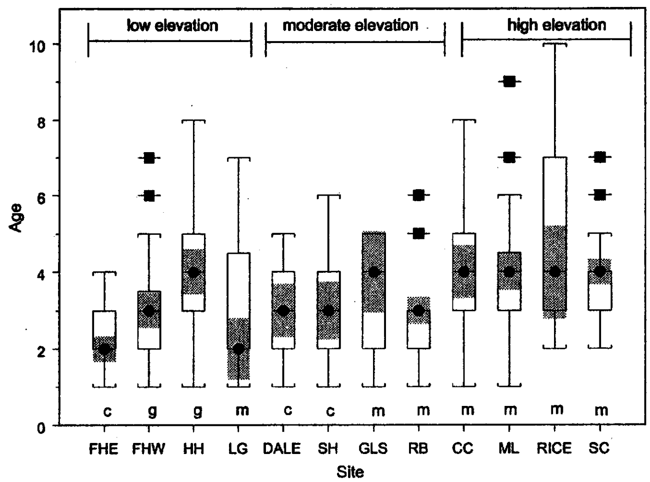

FIGURE 4. Box plot of the ages for the 12 sample sites arranged by disturbance class (Abbreviations c, cultivated; m, mechanically disturbed; g, grazed) and elevation class (l, low; m, mid; h, high). Shaded areas represent the 95% confidence limits about the median, thin lines represent the range of ages, and square solid boxes are outliers.

year (C. G. Parks, unpublished data). The interpretation of the stable age distribution would be that a population is self-replacing under assumed constant recruitment, transition, and mortality rates (Gotelli 2001; Harper 1977; Leak 1965). Although these assumptions are seldom strictly met in reality, this theoretical model is reasonable for invasive plants that exhibit patterns of increasing population densities across regional scales. Future age-related research and increased sampling is needed to understand the demography and age structure of rosettes and seedlings. Such studies, coupled with estimates of germination success, may be useful for forecasting a population growth rate for large landscapes.

Relationships among Size, Reproductive Characteristics, and Plant Age

There were no correlations among reproductive parameters (total number of flowers per plant, number of flowers per stem), vegetative parameters (number of stems per plant, plant height), and plant age or age class for the 12 sampled populations. Mean number of flowers produced per plant from all sites was 57 (± 51 SD), with the number of flowers ranging from 0 to 411. In a separate study conducted at some of the same sites, the average number of sulfur cinquefoil seeds per flower was found to be 107 ± 20, and seed production was estimated to be nearly 6,000 seeds per plant (Dwire et al. in press). Our study results indicate that sulfur cinquefoil plants have the ability to produce seeds during their first year and reproduce throughout their life spans at a constant rate. This information helps explain the rapid spread of sulfur cinquefoil after initial establishment.

Plant height ranged from 25 to 76 cm across the 12 sites, with a mean of 45 cm (± 9.17 SD). One-year-old plants exhibited the same range of heights as older plants. Mean number of stems per plant was 2.6 (± 1.8 SD) and ranged from 1 to 11 stems per flowering plant. One-year-old plants and the oldest age class had slightly fewer stems than middle-aged plants. Thus, whereas the age of sulfur cinquefoil plants may be determined readily from ring counts in the root crown, plant size and flower production are not indicative of plant age.

Sulfur Cinquefoil Age and Site Characteristics

Median plant age was positively correlated to elevation (R^2 = 0.50, $P < 0.01$). The four highest elevation sites showed a greater number of older plants in age distributions as displayed in box plots (Figure 4). At our study sites, higher elevations are characterized by cooler and moister environmental conditions that may favor establishment and longevity of forbs, but increased sampling over a broader range of elevations is needed to clarify relationships.

There was no relationship between disturbance class (cultivated, grazed, and mechanical) and age or age classes. The mechanically disturbed and cultivated sites arguably were the most altered, (soil displacement and chronic compaction by heavy equipment), but the grazed sites are also considerably disturbed due to repeated trailing and potential compaction, which may partially explain the lack of correlation between age and disturbance type. Furthermore, all sites have been and continue to be chronically grazed by wild ungulates. Two adjacent slope sites were bisected by a road with the upslope site, FHW, having an earlier establishment date (1995) than the downslope site FHE (1998). The FHE site, which was a near monoculture of sulfur cinquefoil when sampled in 2001, had last been cultivated in late fall of 1996. Cultivation has been determined to effectively eradicate adult plants (Rice 1999), so we assume that FHE was colonized from a nearby seed source (FHW) or by a residual seed source (i.e., plants recruited from the seed bank that survived cultivation).

Some type of disturbance usually precedes the establishment and spread of invasive plants in native plant–dominated communities (Fox and Fox 1986; Hobbs 1989; Hobbs and Huenneke 1992). Disturbance creates patches of open ground or increases the availability of one or more limiting resources. Disturbed sites are reportedly particularly susceptible to early colonization and rapid dominance by sulfur cinquefoil (Hickman 1993; Lackschewitz 1991; Rice et al. 1999). Although our results did not show a relationship of sulfur cinquefoil population age with disturbance type on our study sites, there is indication that disturbance was associated with population establishment as illustrated by the FHE population in which plants established the second year following final cultivation.

Conclusions

Determining the age structure of invasive plant populations is a promising application of herbchronology. Herbchronology provided insight into sulfur cinquefoil invasion biology and showed that a 1-yr-old plant (i.e., new invader) may produce as many seeds as a well-established, older plant. This information helps explain the rapid spread of sulfur cinquefoil at a site. We suggest that the management of sulfur cinquefoil should focus on reducing seed sources, early detection of colonization, and rapid responses to invasion. Because sulfur cinquefoil age distributions were continuous, with all age classes represented, we suggest that the species is able to perpetuate itself once established. Future research could concentrate on mapping plant ages to track changes in population structure and on comparative analysis of co-occurring native plants to gain insight into demographic characteristics that make sulfur cinquefoil a troublesome invader.

Sources of Materials

[1] American Optical microtome model 860, American Optical Company, Instrument Division, Buffalo, NY 14215.

[2] Toluidine blue O, Sigma-Aldrich, Co., P.O. Box 355, Milwaukee, WI 53201.

[3] SPLUS 6.1 statistical software (2001), Insightful Corporation, 1700 Westlake Avenue, North Suite 500, Seattle, WA 98109.

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