Invasive Plants: Ecological and Agricultural Aspects
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Defining a regional approach for invasive plant research and management

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Introduction

Invasive plants are now recognized as a serious threat to most extensive management systems, such as forests, meadows, deserts, and riparian areas [1–3]. Vitousek et al. [3] described exotic plant invasion as a significant element of global environmental change because exotic plants can alter primary productivity, decomposition, hydrology, nutrient cycling, and natural disturbance regimes. Non-native plants also impact landscapes by changing the structure, composition, and successional pathways of native communities [3–8].

In North America, preventing, reducing or eliminating undesirable impacts of non-native invasive plants is a difficult challenge facing public and private land managers. Non-native plants account for about 65% (over 1,350 species) of the total number of invasive species in the United States and impacts to the US economy are believed to exceed $13 billion per year [9]. In the Pacific Northwest Region (PNW, Fig. 1), non-native plant invasions began in the mid-1800 s with the arrival of European settlers. Non-native invasive plants initially spread through contaminated crop seeds, a rapidly developing railroad system, and often-intense livestock grazing [10]. More recently, road building, road use, logging, grazing, forage seeding, certain erosion control practices, fire rehabilitation measures, and irrigation ditching facilitate the spread of non-native invasive plants [11–13]. Harrod [8] reviewed the effects of invasive plants on land management in eastern Oregon and Washington, and found that 65 plant species in the Blue Mountains (Fig. 1) were listed as "noxious weeds" by federal and state agencies. The Invaders Database [14] lists 53 non-native plant species characterized as noxious that are found in eastern Oregon. An additional 16 non-native species to those found in eastern Oregon were characterized as noxious in Idaho and Washington (Tab. 1).

Because of the serious invasive plant problem in the PNW, there is a need to develop research programs than span biological and spatial scales while at the same time facilitate relationships between scientists and land managers. This is not easily accomplished and requires considerable coordination and communication. In this paper, we present a framework for research that can be

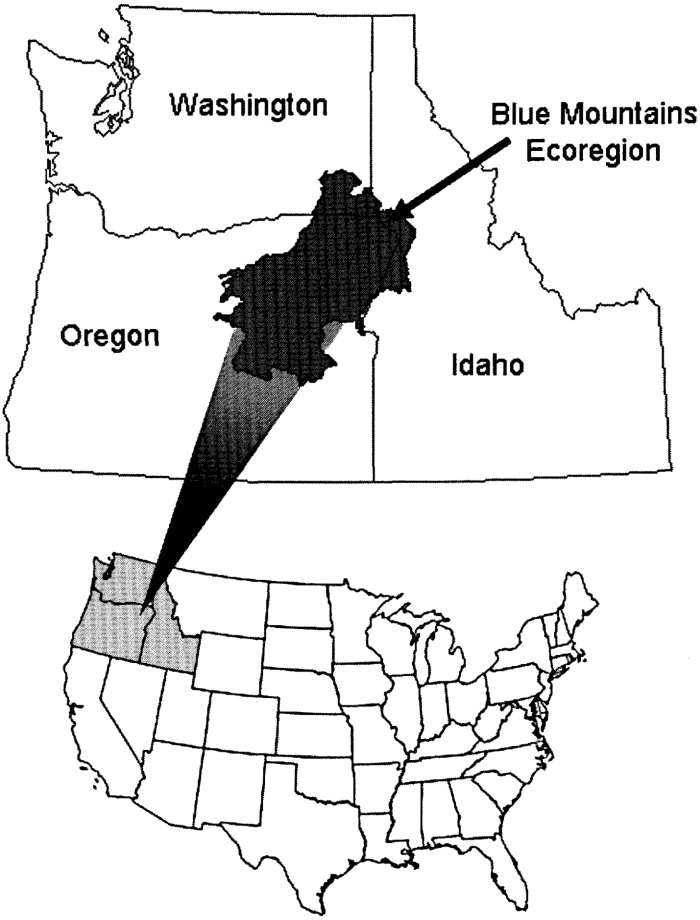

Figure 1. The Blue Mountains Ecoregion is represented in the three states that form the Pacific Northwest Region of the United States – Oregon, Washington, and Idaho.

valuable for directing and conducting regional invasive plant management. The proposed approach strengthens partnerships between researchers and land managers and can result in effective, responsive invasive plant management and habitat restoration programs.

Components of a regional research framework for invasive plant management

Empirical studies and observations of non-native exotic plant invasions can greatly assist development of management programs for prevention, containment or eradication of particular invasive plant species. Such management pro-

Table 1. Noxious exotic plant species occurring in Idaho, Oregon and Washington east of the Cascade Range [101]. Noxious weeds are species specified by law as being especially undesirable, troublesome, or difficult to control; precise definitions vary according to state laws and legal interpretations.

Latin name	ID	OR	WA	Latin name	ID	OR	WA
Abutilon theophrasti		•	•	*Hyoscyamus niger*	•		•
Aegilops cylindrica	•	•	•	*Hypericum perforatum*		•	•
Agropyron repens		•		*Hypochaeris radicata*			•
Anchusa officinalis		•	•	*Iris pseudacorus*			•
Anthriscus sylvestris			•	*Isatis tinctoria*	•	•	•
Artemisia absinthium			•	*Kochia scoparia*		•	•
Cardaria draba	•	•	•	*Lepidium latifolium*	•	•	•
Cardaria pubescens	•	•	•	*Linaria dalmatica*	•	•	•
Carduus acanthoides		•	•	*Linaria vulgaris*	•	•	•
Carduus nutans	•	•	•	*Lythrum salicaria*	•	•	•
Carduus pycnocephalus		•	•	*Matricaria maritima*			•
Centaurea diffusa	•	•	•	*Myriophyllum spicatum*	•	•	•
Centaurea jacea			•	*Nardus stricta*	•	•	
Centaurea biebersteinii	•	•	•	*Onopordum acanthium*	•	•	•
Centaurea pratensis	•	•	•	*Panicum miliaceum*		•	
Centaurea repens	•	•	•	*Peganum harmala*		•	
Centaurea solstitialis	•	•	•	*Phalaris arundinacea*			•
Centaurea triumfettii		•		*Polygonum cuspidatum*		•	•
Chondrilla juncea	•	•	•	*Polygonum sachalinense*		•	•
Chrysanthemum leucanthemum			•	*Potentilla recta*		•	•
Cirsium arvense	•	•	•	*Rorippa sylvestris*		•	
Cirsium vulgare		•	•	*Rubus discolor*		•	
Conium maculatum	•	•	•	*Salvia aethiopis*		•	•
Convolvulus arvensis	•	•	•	*Salvia sclarea*			•
Crupina vulgaris	•	•	•	*Secale cereale*			•
Cynoglossum officinale		•	•	*Senecio jacobaea*	•	•	•
Cyperus esculentus		•	•	*Sonchus arvensis*	•		•
Cytisus scoparius	•	•	•	*Sorghum halepense*	•	•	•
Daucus carota			•	*Sphaerophysa salsula*		•	•
Euphorbia esula	•	•	•	*Taeniatherum caput-medusae*		•	
Euphorbia myrsinites			•	*Tamarix spp.*		•	•
Gypsophila paniculata			•	*Tanacetum vulgare*			•
Halogeton glomeratus		•		*Tribulus terrestris*	•	•	•
Hieracium aurantiacum	•	•	•	*Xanthium spinosum*		•	•
Hieracium pratense	•	•	•				

grams can, in turn, be helpful to further identify research needs. Research to inform regional management of invasive plant species requires explicit consideration of scale, while empirical study may be concentrated on species biology, population demography and/or habitat level risk assessment (Fig. 2). This paper discusses the three components necessary to develop a regional approach for invasive plant research and management: 1) an understanding of the steps for plant invasions to occur, 2) consideration of relevant biological and geographic scales, and 3) interaction with natural resource managers. We then present an example research framework to inform scientists and managers about the potential of this regional research approach using the invasive plant *Potentilla recta*.

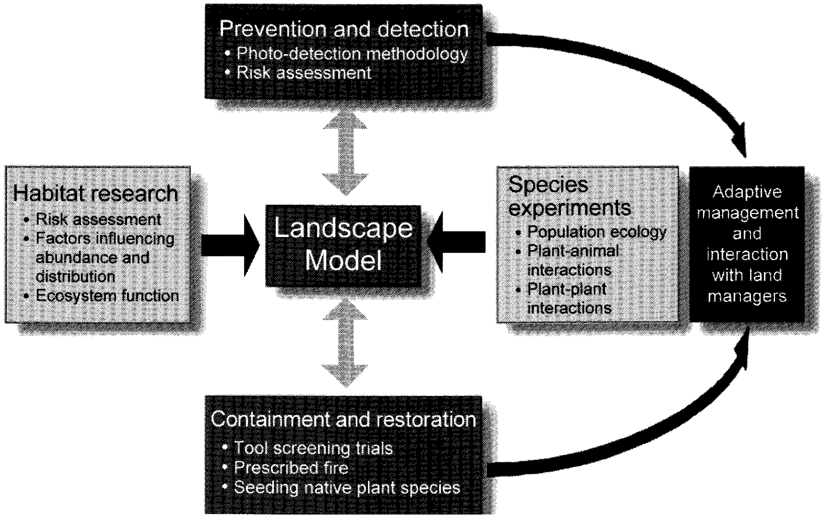

Figure 2. Regional approach for *Potentilla recta* research and management in the Blue Mountains Ecoregion of the Pacific Northwest, USA. The research approach was developed for management of a single species, *Potentilla recta*, and may become more complex as additional species are added to the framework.

Steps of the invasion process

Cousens and Mortimer [15] indicate that the process of plant invasion consists of three phases – introduction, colonization, and naturalization – while Richardson et al. [16] restructure the invasion process into introduction, naturalization and invasion. Richardson et al. [16] reserve invaders as a special plant category whereby exotic plant species occupy and expand into areas without further assistance from humans. Disturbance is generally accepted to be a fundamental factor for successful introductions and colonization/naturalization phases in both classifications [5, 17, 18].

Humans to some degree have modified most of the world's ecosystems, and this has a direct effect on invasibility. Some ecosystems are altered by the presence of exotic plants themselves [19], through an increase in fire frequency, nitrogen depletion or allelopathic chemicals. Other species are adapted to conditions following land use changes, whereas native species are not, e.g., resilience to grazing pressure in the Great Basin of the western United States [20]. An explanation for semi-arid and grassland vulnerability to invasion by exotic plant species is that these areas have spatially open niches, microsites that are devoid of vascular plants for some or most of the year [21]. Plants that have life forms dissimilar to the native vegetation also have invaded some ecosystems. For example, the conversion to annual grasslands from tussock grasslands in California, and the invasion of *Opuntia stricta* into Australia (a cactus where no members of Cactaceae existed previously) are examples where biological characteristics play an important role in the invasion process as well as site factors and disturbance.

Species invasions can generally be depicted by a logistic growth curve [22]. Population growth curves may then be generated for plant species given their initial population size, intrinsic growth rate, and time. Small populations are often undetected during the early introduction phase of invasion because individual plants may remain unnoticed for long periods of time. Dispersed seed must compete with the established flora that is well adapted to the site in the absence of disturbance; thus few introductions proceed to the next phase of invasion. For example, Williamson [23, 24] estimates that only about one percent of all introduced species into the British flora become established and are invasive enough to be considered as pests [25].

Colonization/naturalization [15, 16] is characterized by exponential population growth of the introduced species. During this explosive growth phase, the species often becomes apparent to land managers and control efforts begin. This phase of invasion is closely related to the intrinsic rate of increase for the plant species. Hence, predictions of colonization/naturalization rates and management options should focus on the intrinsic biology of the species. For example, Maxwell et al. [26] divided the life history of *Euphorbia esula* L. into five stages: seed, buds, seedlings, vegetative shoots and flowering shoots. By identifying these stages, the process of population development was determined using a stage-based matrix model. In this way the process of population development and expansion was determined.

Theoretically, at some carrying capacity, K, the species' population approaches a quasi-threshold density where its population growth stabilizes or does not expand quickly. At this point colonization/naturalization is complete. The K density occurs when niche occupancy and available resources limit the rate of species spread, which is controlled by environmental or habitat-level factors like competition or herbivory. Thus predictions of risk for species approaching K also should focus on habitats or the disturbance of them. Table 2 delineates disturbance types important for habitat susceptibility to non-native invasive plants in one of our study areas in northeast Oregon.

Descriptions of biological and environmental characteristics for most invasive species are often lacking or only general in nature. Thus, it is difficult to determine which plant species are most likely to be invasive [1, 10, 27]. Formation of a landscape-level model augmented by empirical study of habitat (environmental) and species (biological) factors can inform the overall program for non-native invasive plant management in extensive production systems (Fig. 2).

Relevant scales and disturbances

Sauer [28] and Forman [29] indicate that ecological processes that determine the function and stability of plant communities during plant invasions are

Table 2. Primary disturbance types that may modify carrying capacity, K, of habitats comprised primarily of native species in the Starkey Experimental Forest and Range, Oregon

Disturbance	Affected plant communities
Fire (prescribed and wild)	Grand fir, Douglas-fir, mixed conifer, ponderosa pine, lodgepole pine, bunchgrass, Sandberg's bluegrass, Idaho fescue, wet meadow, low sagebrush, and juniper communities
Livestock grazing	Plant communities within current grazing allotments, including grand fir, Douglas-fir, mixed conifer, ponderosa pine, lodgepole pine, bunchgrass, Sandberg's bluegrass, and Idaho fescue communities
Timber harvest, fuels reduction, or canopy thinning activities	Grand fir, Douglas-fir, mixed conifer, ponderosa pine, and lodgepole pine stands
Roads	All plant communities

scale-dependent and range from individual species to landscapes. Land managers need research that incorporates both specific biological and habitat-level inputs over a broad landscape. Scales too large to detect local-level invasions or too small to find and monitor invasive plants effectively are, therefore, of limited use. Management policies for invasive plants are developed best for broad regional scales, while managers require tools that directly aid detection, monitoring, and containment of invasive plants at scales small enough for eradication or control (Fig. 2).

Species

A regional research program to implement prevention tactics or control and restoration after exotic plant introduction must necessarily focus on the biology of the invading species and steps of the invasion process (above). However, the species is also likely to affect the composition of plant communities (habitats), and thereby the functions and patterns of those ecosystems and landscapes that are invaded.

Habitat

Habitat characteristics and their modification often have a direct bearing on the success or failure of particular invasions [30]. The environmental factors most responsible for floristic growth and persistence of invasive plant species are soil, climate, and land use.

Many studies show that plant growth and invasive plant prevalence occur within certain ranges of habitats [31], and usually species are most productive within certain soil types. Although soil classification can be used to study and develop predictive landscape-level models of plant invasions, soil mapping units of extensive land management systems are generally too coarse to be of use for that purpose. In addition, other microsite factors such as small mounds or ephemeral pools may play a role in the overall invasive process. However, such fine-grain factors are also difficult to quantify for landscape-level models or habitat-level risk assessments [32]. Climate also drives abiotic and biotic thresholds for plant growth in particular ecosystems. For example, the retreat of forests to mountainous areas over the last 10,000 years is a direct result of changing climate [33]. Climate can also change habitat suitability over short timescales through drought, seasonal frost, and flooding [34]. Invasive plant species tend to adapt well to a variety of habitats but usually invade regions with similar climates to their native range first, then adapt to other climates later [35]. Edaphic characteristics such as topography and elevation modify climate, and therefore influence the plant species that can grow at a given location. Land use and the resulting condition of the environment is a third driving component of habitat suitability and invasion. Changes in land use are thought to be the single most important factor in species extinction [15] and to have strong influences on invasible sites [36].

Landscapes

Across a region, a species may be detected in the late colonization/naturalization or early naturalization/invasive phase [15, 16] and thus be considered a stable population. However, this stable source population contributes to many subsequent local infestations through seed dispersal. These small satellite populations are sinks from the source and can become additional source populations themselves, which expand markedly from the original infestation area [37]. Rates of increase for satellite populations can be extremely high because satellite introductions have a much higher probability of success than initial introductions as a result of the constant seed flow that arises from source areas [38, 39].

Landscape features and connectivity relationships become important for predicting spread from source populations to new and as yet unoccupied locations for exotic plant species. Regions are composed of a mosaic of extensive natural resource areas (forests, rangelands, wetlands, etc.), intensively managed locations (farms, paddocks, holding areas for livestock, etc.), urban areas of various sizes (intensities), and the corridors (roads, rivers, etc.) that connect them all [32]. Invasive plants can be present in each landscape feature. The spread of *Bromus tectorum* across most of the western United States since 1900 [40], and the replacement of native hardwood forests in Australia and other regions of the world by *Pinus radiata* [41] are important examples of landscape change by exotic plant species. Transportation corridors can markedly influence the risk associated with species spread as satellite populations [42].

Interaction with land managers

Scientifically rigorous research is fundamental to a regional research program, but the gap between scientific knowledge and existing management practices must be narrowed for invasive plant management to be most effective. There is a need for biological, ecological and social knowledge to inform decisions (Fig. 2). The use of science adds credibility to management decisions, providing conceptual approaches for complex problems and contributes to new techniques for accomplishing management objectives. However, efforts to inform managers about scientifically derived knowledge and conceptual approaches are often applied *ad hoc*, with most scientific information provided in the form of publications and presentations. Interaction among scientists and managers, working together to ensure that research is pertinent and effectively applied, is most likely to result in success (Fig. 3).

Adaptive management (Fig. 3), whereby management practices are continuously reassessed and modified as new information becomes available, is an appropriate approach to manage invasive plant species [43]. Research can be advanced by partnerships between scientists and land managers, where managers identify concerns and provide information about day-to-day management activities. Direct scientific feedback from researchers also hastens the progress of adaptive management [44–46]. In addition, designing and conducting research in collaboration with local land managers can result in increased applicability of the research [47].

Awareness of regional invasive plant species allows land managers to recognize invasions at early stages. Studies show that invasive species have a lag time, often taking several decades to expand during which they grow in small, isolated populations and do not spread [48, 49]. Non-native species that are not

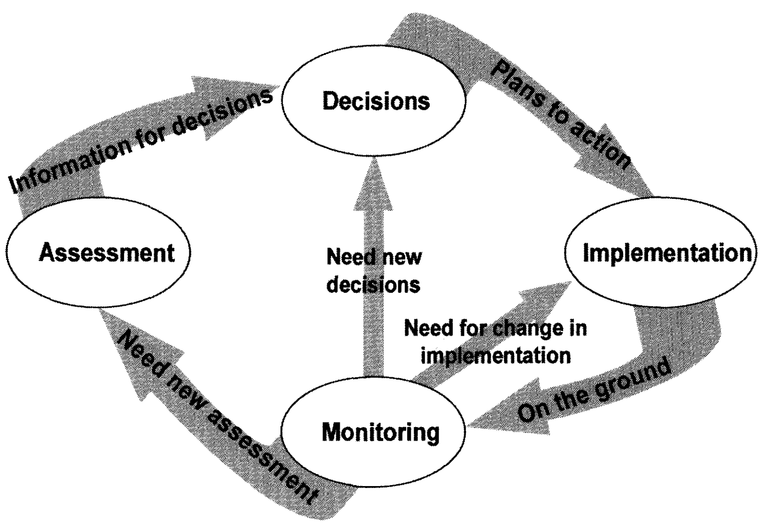

Figure 3. Adaptive management approach for a regional research program that depends on land manager feedback. Modified from [102] for invasive plant management.

currently considered invasive can eventually affect ecosystem function. Thus, it is important to consider the potential impacts of all introduced plants, not just those already discovered or deemed invasive. Including scientists, conservation managers, and local botanists in defining research and management priorities improves detection of a broad range of introduced plants.

Example research framework: *Potentilla recta* in the Blue Mountains Ecoregion of North America

There are many noxious exotic plants presently occurring east of the Cascade Mountains in the Pacific Northwest (Tab. 1). However, only some of these species are considered invasive over large areas, while others are more restricted in distribution. Managers and policy makers want to know the likelihood of new plant species becoming prevalent over large areas, but ecologists are only able to provide after-the-fact explanations for invasions. Predicting which species will be invasive and which habitats and ecosystems are invasible remains difficult [24]. *Potentilla recta* (Tab. 1) is a relatively recent introduction to the PNW with many new infestations reaching environmentally severe sizes and densities [50]. Despite widespread concern about *P. recta,* we were unaware of any ongoing studies, and only sparse information was available in the literature to inform managers about the species.

Potentilla recta (Rosaceae, common name is sulfur cinquefoil) is a herbaceous perennial forb native of Eurasia. It was introduced to North America prior to 1900 [51], and has since spread across the continent. It has been reported in all states of the USA, except Arizona, Utah and New Mexico. The ten Canadian provinces also have documented the presence of *P. recta*. The plant reproduces only by seed, has a single taproot, and may have several shallow, spreading branch roots, but no rhizomes. *Potentilla recta* has four general life history stages [52]; viable seed in the soil, seedlings, non-reproductive rosettes, and reproductive stemmed individuals [53]. Werner and Soule [54] provide information on the biology of the species from early observations made in eastern North America where *P. recta* is a minor agricultural weed. More recently, *P. recta* is recognized as increasing in the drier climates of northwestern North America and is considered a threat to native plant communities where it forms dense populations [50, 55, 56].

Dense and continuous *P. recta* populations most commonly occur on areas of soil disturbance (e.g., old fields), but increasingly, populations have been observed in rangelands and in the understory of open-canopied ponderosa pine forests. *Potentilla recta* is unnoticed in many parts of its range because it is similar in appearance to native co-occurring congeners, particularly *Potentilla gracilis* [50]. There are no available biological control agents for *P. recta*. Due to the plant's close genetic relationship to native *Potentilla* species and to cultivated strawberry, finding a host-specific biocontrol agent for *P. recta* is therefore difficult. *Potentilla recta* was first reported in northeast Oregon in 1969.

The research described here is being conducted in the Blue Mountains Ecoregion of the interior PNW (Fig. 1). It consists of interrelated studies to assess habitat risk, project species population spread, and determine the life cycle, dispersal, competition, and containment strategies of the species. Figure 2 depicts the interrelationships of these studies within our regional invasive species research framework. We now briefly describe our ongoing research and how these studies are used to develop a landscape-level projection of range expansion (Fig. 2) and management of *P. recta*.

Habitat-level research

Information on the underlying factors that influence *P. recta* abundance [53, 54, 57] indicates the species has broad ecological amplitude, yet no quantitative assessment of which factors most strongly influence *P. recta* abundance had been conducted. A study was implemented using a geographic information system (GIS) to examine possible relationships between *P. recta* occurrence and environmental, historical and landscape variables. These variables included habitat type, vegetative canopy cover, slope, elevation, aspect, general soil type, land use history (disturbance), and proximity to roads. Information from this study provided insights on the relative contribution of the various factors to *P. recta* occurrence and relative abundance, and is now integrated into the risk assessment and landscape projections of species expansion described below.

Risk assessment

Anticipating species that may become invasive in particular landscapes and knowing where to look for them is a particularly important aspect of invasive plant management. Byers et al. [44] identify four stages of invasive plant risk assessment for biological invasions of non-indigenous species to occur: 1) arrival (risk associated with entry pathways), 2) establishment (risk of forming viable, reproducing populations), 3) spread (risk of expanding its extent), and 4) impact (risk of having a measurable effect on existing species or communities).

At the Starkey Experimental Forest and Range (SEFR) a risk assessment (Figs 2 and 4) was conducted to determine what habitats are at risk to *P. recta* invasion. SEFR encompasses 7,762 ha with elevations ranging from 1,122–1,500 m in northeastern Oregon. Major plant associations (habitats) include *Abies gradis*, *Pseudotsuga menzeisеii*, *Pinus ponderosa*, *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Poa sandbergii* communities. Habitats at risk to *P. recta* invasion were found by integrating three components of habitat vulnerability using GIS technology. The three components are: 1) *Susceptibility* – vulnerability of each habitat to *P. recta* establishment. Susceptibility was determined for each habitat found in SEFR using reports of *P. recta* occurrence in other areas of the Blue Mountains; 2) *Disturbance his-*

tory – includes livestock grazing allotments, sites of prescribed or natural fires, timber harvest, fuels reduction or thinning activities, roads, and other activities that physically disturb the soil or vegetation (Tab. 2); and 3) *Proximity of current infestations* – location of known populations of *P. recta* mapped using global positioning systems (GPS) tools.

The three GIS data layers were then integrated to determine the areas at risk to *P. recta* invasion within SEFR (Fig. 4).

Risk assessment (e.g., Fig. 4) is a valuable tool for land managers to prioritize prevention, containment or control activities. For example, a land manager may choose to contain exotic plant populations that are within high-risk

Figure 4. Areas at varying risk to invasion by *Potentilla recta* in Starkey Experimental Forest and Range. Risk depends on the integration of habitat susceptibility, disturbance, and proximity to current infestations.

habitats as opposed to treating multiple infestations that have little potential to spread to adjacent low-risk areas (Fig. 4). Prevention activities are also enhanced by such assessments because managers can direct their inventory and monitoring activities to high-risk areas for early detection and rapid eradication of small exotic plant populations.

Such analyses are also useful for directing the research effort. As our assessment progressed, it became evident that seed dispersal was critical for expansion of *P. recta*. As a result, studies to identify mechanisms of short- and long-distance seed dispersal of the species were initiated and are now being used to make future risk and expansion assessments.

Species-level experiments

In the interior PNW, invasive species such as *C. biebersteinii*, *C. solstitialis*, and *E. esula* have received considerable attention from ecologists and land managers [58, 59]. Relatively little is known, however, about other invasive plants listed in Table 1. Without an understanding of the biology of the species, it is difficult to assess the ecological implications of introductions, determine population expansion rates, or develop appropriate approaches for eradication, containment, or restoration.

Age structure

Age provides the timeline needed to determine population dynamics and patterns of species persistence. It is also frequently related to reproductive potential and size of the species, and defines longevity. Perkins et al. [60] determined the age structure of *P. recta* populations in northeastern Oregon by counting root annual-growth-rings to estimate the age structure of the populations, relate plant size and flower production to plant age, and examine the relation of population age structure to environmental variables and disturbance history. Results from this study indicate that in the Blue Mountains *P. recta* adults average 3.5 years old and range in age from 1 to 10 years. Age was not related to number of flowers, plant size, or site disturbance type, but was positively correlated with site elevation [50, 60].

Life history, demography, and population dynamics

The life history of a plant characterizes its stages of development through germination, growth, reproduction and death. Such demographic attributes influence the population spread, range expansion and subsequent management of invasive species. The population dynamics of *P. recta* were studied by monitoring tagged individuals for 2 years. During this time, plant size, growth, survivorship, and seedling recruitment were tracked, providing information to estimate population growth rates using a population matrix model (Tab. 3).

To construct a population matrix model (Tab. 3), three parameters were determined for each life history stage: 1) the probability that an individual will

Table 3. Example transition matrix for *P. recta* in northeastern Oregon, yielding a population growth rate (λ) of $\lambda = 1.2144$. The population is increasing by about 21% annually.

Year 2	Year 1				
	Seed	Seedling	Rosette	Small adult	Large adult
Seed	0	0	0	1211	3528
Seedling	0.001	0	0	0	0
Rosette	0.001	0.05	0.55	0.16	0.02
Small adult	0.0001	0.01	0.21	0.43	0.35
Large adult	0	0	0.01	0.11	0.46

survive and remain within that size class for a year, 2) the probability that an individual will survive and grow into another stage and 3) reproductive output or fecundity [61]. The model (Tab. 3) describes a variety of population parameters including the population growth rate (λ). Initial analyses indicate that *P. recta* populations in old fields expand at about 21% per year.

Relative growth rate and competitive ability

Growth analysis is a methodology to determine plant carbon allocation patterns over time, which may influence competitive ability with other plants in a community. Relative growth rate (RGR) is a measure of dry matter accumulation in relation to size of the individual over time; it is the efficiency of plant growth through time [62, 63]. Tuitele-Lewis [64] determined RGR for *P. recta* over a range of disturbed and undisturbed conditions on three old-field sites in the Blue Mountains Ecoregion. He found that *P. recta* ranged from 0.52–1.01 g g^{-1} $week^{-1}$ for the three sites in 2002, and 0.13–0.2 g g^{-1} $week^{-1}$ in 2003. These values were not unusual when compared to those of other common plant species in the area that were obtained from the literature (Tab. 4). It appears that RGR, as a measure of individual plant resource acquisition, is not

Table 4. R_{max} for certain plant species found in the Blue Mountains of northeast Oregon [64]

Species	R_{max}	Author
Bromus tectorum	0.51 g g^{-1} d^{-1}	Arredondo et al. [98]
Taeniatherumcaput-medusae	0.43 g g^{-1} d^{-1}	Arredondo et al. [98]
Pseudoroegneria spicata	0.36 g g^{-1} d^{-1}	Arredondo et al. [98]
Elymus elymoides	0.41 g g^{-1} d^{-1}	Arredondo et al. [98]
Phleum pratense	0.23 g g^{-1} d^{-1}	Poorter and Remkes [99]
Achillea millenifolia	1.96 g g^{-1} $week^{-1}$	Grime and Hunt [100]
Festuca rubra	1.18 g g^{-1} $week^{-1}$	Grime and Hunt [100]
Potentilla recta	0.83 g g^{-1} $week^{-1}$	Grime and Hunt [100]

an important factor accounting for the ability of *P. recta* to dominate certain forest and meadow sites in northeastern Oregon.

Seed dispersal

Dwire et al. [65] quantified seed production and measured seed dispersal of *P. recta* in different habitats in northeast Oregon. Seed dispersal was measured by using sticky traps that surrounded individual source plants. Seed production, distance of seed dispersal, and timing and duration of seed dispersal were measured. Results indicated that the 83% of the seeds that were produced dispersed within 60 cm from the mother plant. This is an insufficient distance to adequately explain the rapid spread of *P. recta* across the region and dispersal over longer distances than 60 cm appears to be critical for *P. recta* spread. Newbert and Caswell [66] and Caswell et al. [67] indicate that dispersal of relatively few seeds at the edge of an expansion 'wave' can account for the rapid spread of many invasive organisms (Fig. 5). Therefore we are initiating other studies to identify mechanisms of longer-distance dispersal of this and other plant species.

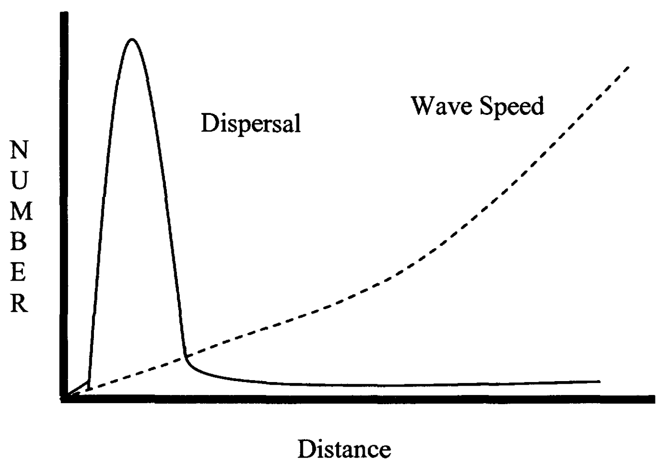

Figure 5. Hypothetical relationship of dispersal distance to dispersal wave speed.

Dispersal and herbivory

Domestic and wild mammal and avian herbivores may contribute to plant invasions by seed transport of invasive plants into previously uninhabited sites through endozoochory [68]. This phenomenon occurs when animals consume seeds in one area and later regurgitate or defecate them in another. Invasive species with thick seed coats dispersed by endozoochory, in addition to benefiting from transport, may have enhanced germination as a result of scarification in the gut [69]. Invasive plant seeds, including those of *E. esula, Crupina vulgaris, C. biebersteinii,* and *Lonicera maackii* have been recovered from feces and found viable in numerous studies [70–73]. Observations at our study sites suggest that ungulates may be the primary dispersers, as they browse *P. recta* seed heads in the fall [74]. To verify these observations, studies are underway to determine whether herbivores (cattle, elk, deer, quail, wild turkey) consume and transport viable *P. recta* seeds.

Beyond abilities to disperse seeds, ungulates have profound impact on the structure and composition of plant communities [75, 76]. However, the role of ungulates as contributors to the establishment and spread of non-native invasive plants is not well known. Little information is available on use of *P. recta* by ungulates, although it is reportedly avoided by most grazing animals [50]. Despite reports suggesting that *P. recta* is minimally grazed, substantial ungulate herbivory of the species in infested areas of northeastern Oregon have been observed. A study is in progress to determine whether grazing by cattle or native ungulates directly or indirectly affects the density and demography of *P. recta*. This study employs three grazing treatments – extant grazing (cattle, elk, and deer herbivory), deer and elk herbivory only, and total exclusion.

Pollination

The spread of an invasive plant species, especially those that reproduce only by seed, may depend on how successful plants are at competing for the service of resident pollinators. Basic information on the pollination biology and ecology of most invasive plant species is lacking. This information is necessary especially for those species that require out-crossing to produce viable seed. The sparse literature available on pollination biology of *P. recta* indicates that *P. recta* can set seeds without pollinators and that fewer but larger seeds are produced on pollinator-excluded plants [54]. McIver et al. [77] are defining the insect pollinator community for *P. recta*. This research evaluates the dependency of *P. recta* on insect pollinators for seed production compared to co-occurring native *Potentilla* species. Pollinator-excluded plants are evaluated for seed set, seed size, and germination rate. Flower quality comparisons rate the ability of *P. recta* and native *Potentilla* species to attract pollinators via pollen and nectar production. The degree of fidelity of pollen transfer within and among *Potentilla* species is being determined. Results thus far have found that *P. recta* produces flowers with nectar richer in sugar and seed heads twice the mass as compared to native *Potentilla* species. Final results from this study will help clarify *P. recta* reproductive ecology and the ecological relationship of *P. recta* with other species within the community it invades.

Interference/competition

Plant mortality, growth, and fecundity, are key biological mechanisms that can provide insight into the way invasive species affect the habitats into which they are introduced [78–80]. This is especially true if the mechanisms are density dependent [81]. If density dependence is a factor in the overall ecological success of a species, whether a plant is density dependent to its own or another species can determine the manner in which the new plant community evolves. The impact of the invasive plants on ecosystem function might then be examined by the degree of niche overlap among the co-existing species as determined by their responses to separate and combined densities. *Potentilla recta* is a highly successful plant species that effectively displaces native vegetation in certain habitats of northeastern Oregon. However, little empirical evidence exists about the mechanism by which such displacements occur.

To clarify the competitive relationship of *P. recta* and other plant species over a range of habitats two experiments were established. In the first experiment the competitive relationship of *P. recta*, *P. gracillis* (a native *Potentilla*), and *Pseudoroegneria spicata* (a native grass) is being examined in an addition series experiment [82, 83]. Various densities of each species are planted alone and in mixtures and by analyzing the effects of the resulting species ratios on mortality, biomass accumulation and reproduction, the interaction among the species can be determined. The second ongoing study is a diallel experiment [82, 83], where intra- and inter-specific combinations of the three species are planted in a variety of habitats (e.g., wet meadow, dry meadow, and open-canopy forest) and elevations. Data from both experiments will be used to determine yield ratios and competitive ability among the species, and should illuminate plant-plant interactions for disturbed and undisturbed areas and site conditions.

Landscape model

Modeling weed infestations has been attempted in numerous studies during the last decade with varying success [38]. Predictive models thus far have generally used analytical diffusion equations in an attempt to apply any weed species to any area [84, 85]. However, both biological (species) and environmental (habitat) factors form the baseline to determine the invasion risk and subsequent spread of non-native plant introductions. Modeling to assess the risk and spread of plant invasions should be at this interface of a species' biology and the speed at which it can occupy habitats as modified by environment, land uses and disturbances [38, 66]. Development of a prototype cellular automata-type model to project geographic spread of *P. recta* and other invasive plant species in the PNW (Fig. 2) is underway following the theoretical papers of Caswell and associates [66, 67, 86]. This landscape model couples a population matrix that describes population growth (e.g., Tab. 3) with an integrodifference equation [66] to account for species seed dispersal wave speed (Fig. 5) at which an exotic plant population, such as *P. recta*, might expand.

Requirements for the model are life stage parameters to calculate the dominant eigenvalue for population growth of the exotic species (Tab. 3) and a determination of propagule dispersal distance or wave speed over the life cycle of the plant [65]. When these calculations are combined with a GIS risk assessment (e.g., Fig. 4) it should be possible to project areal expansion of the species over time. Such determinations for exotic invasive species are invaluable to land managers because the consequences of management or no action can be determined and policies justified.

Management-level studies

Land managers are responsible for a wide range of actions in response to plant invasions including invasive plant mapping, monitoring, and habitat treatment and restoration. However, the tools available for managers to effectively address plant invasions are limited and invasive plant research programs can play a valuable role in the development, application and evaluation of tools, methods and approaches that land managers might use to manage plant invasions. Traditionally, the development of tools for land managers has not been the focus of invasive plant research projects. Moreover, many invasive plant research efforts have been unresponsive to land manager needs and biased toward small-scale, short-term results in sometimes artificial environments, which thereby limits their applicability [47]. The applicability of many invasive plant research projects have also been limited because they often fail to incorporate interacting, complex processes that operate at large scales (e.g., fire, herbivory, succession, land use change, disturbance corridors such as roads and riparian zones) that land managers must explicitly consider in their management programs. Within our research program, we attempt to overcome these obstacles by initiating research projects designed to develop tools and approaches for invasive plant prevention, detection, control and restoration.

Prevention and detection

A critical question central to invasive plant management is "How can managers accurately and cost-effectively inventory and monitor non-native invasive plants across large landscapes?" This question is particularly important since many non-native invasive plants are easiest to control when populations are small. Owing to limited finances and personnel to sample, inventory, and monitor large areas, the development of methods such as remote sensing to detect invasive plant species is needed.

A wide range of remote sensing techniques have been utilized to detect invasive species, from coarse-scale satellite imagery to fine-scale aerial photography taken from fixed-wing aircraft. Processing and analysis varies from photo-interpretation techniques used to identify invasive species infestations by color, pattern, shape, or photo-texture, to analyses of spectral signatures using image-processing software. Despite the advocacy of remote sensing as a key to early detection of plant invasions, the results have generally been mixed [87–91], and may be of best use over large landscapes with limited access such as wilderness and roadless areas.

To detect *P. recta* infestations in open forest and grassland plant communities in the Blue Mountains Ecoregion, Naylor et al. [92] evaluated natural color aerial photography at three spatial scales. Natural color aerial photography is one of the least expensive remote sensing approaches and color photographs are widely available. For example the Oregon Department of Forestry regularly collects color photographs for a wide range of resource applications. The objectives of this study are to 1) evaluate aerial photography effectiveness in detecting and estimating percent cover of *P. recta*, 2) determine the minimum percent cover of *P. recta* detected at each flight scale and 3) assess this detection method as a tool for resource managers. Naylor et al. [92] indicated that natural color aerial photography can be used to identify *P. recta* populations, even at low densities and is most effective in grassland communities or open forests with little canopy cover to inhibit detection. Future research may employ this technology to analyze more remote areas for *P. recta* invasion.

Containment and restoration

Containment and restoration experiments are critical when promoting regional invasive plant management research programs. There are, however, significant conceptual and logistical challenges to implementing scientifically sound restoration research. Michener [93] reviews these constraints and discusses appropriate research approaches and analytical tools for ecological restoration research.

In areas where invasive species are already well established, tools for effective containment and restoration activities are needed. In the past, weed control strategies that focused solely on the eradication of undesirable species by herbicide or fire often failed, as other weeds quickly colonized the area [58]. For decades, herbicides have been an integral part of invasive species management. For example in 1997, 25% of the 988 million acres of rangeland in the United States, were treated with herbicides [94]. The application of herbicide alone, however, is rarely successful in controlling invasive species. In the short term (1–5 years), herbicides may reduce invasive species abundance, although in the absence of a source of native seeds the treated area is often recolonized by the same species or by other invasive plants. For example, areas treated with herbicide for *Centaurea* spp and *E. esula* control often become dominated by *B. tectorum*, thus further stressing the plant community [94]. As a result, management approaches that integrate invasive species control with habitat restoration through the evaluation of integrated containment/restoration activities are of most value.

Little information exists to indicate whether herbicides are effective in reducing *P. recta* abundance and vigor, or whether subsequent sowing of native seeds facilitates the establishment of native species on treated areas. Consequently, a study was established to address which herbicides, rates, and timing of application are most effective to control *P. recta*, while minimizing impacts on native plant species. A further objective is to determine if post-herbicide reseeding facilitates native plant establishment. This study involves screening six herbicides at two rates of application over three application periods on sites with extensive *P. recta* infestations (densities often > 100 stems/m^2). Following herbicide applications, half of each plot was sown with a native grass seed mix. A range of response variables, including *P. recta* control, and native and non-native species abundance and richness, were recorded [95]. Plots are being monitored for several years to understand longer-term implications of various herbicide and seeding treatments.

To complement the herbicide screening study, an experiment was established to examine the importance of prescribed fire, herbicide application, and native grass seeding on grassland restoration. In the PNW few studies have been conducted on the response of invasive plant species to fire, and only one limited study has explored the effects of fire on *P. recta* [96]. This information is helpful to land managers because it remains unclear if fire, an increasingly popular management tool, facilitates, inhibits or has no effect on the spread of *P. recta*. Basic information on plant species and community responses to fire are necessary for resource managers to assess ecological conditions and trends following treatments, and for the development of post-fire management strategies that enhance plant community restoration, wildlife habitat or other components of biological diversity. In this study [97], three prescribed fire treatments (spring, fall, and no burn) were used in combination with sowing a mix of six native grass species and the application of the best performing herbicide (over 1 year) from the previously described herbicide screening experiment. Reductions of *P. recta* abundance and change in overall community structure and composition, including native plants, are being evaluated.

Integrated tool experiments that combine invasive plant control with restoration activities are likely to be more successful in creating sustainable plant communities in the long-term. This study of fire, herbicide, and restoration seeding, supports information on the ecology of *P. recta*, and provides data on the species' response to fire, herbicide, and native seeding. Results from this study provide land managers, especially those interested in promoting native plant communities, guidance to integrate herbicides, fire, and native plant seeding into an overall invasive plant control program.

Adaptive management and interaction with land managers

Conducting scientifically rigorous research is fundamental to our regional research framework on invasive plant species. Scientific expertise from various sources is being coordinated with land managers to produce information about areas that are at-risk, human uses, and the land values associated with those areas.

Land managers involved in our program represent the United States Forest Service, United States Bureau of Land Management, Oregon Department of Fish and Wildlife, Oregon Department of Forestry, The Nature Conservancy, local weed management districts and private companies and landowners.

These managers provide on-the-ground concerns and information about day-to-day management activities while direct feedback from researchers hastens the process of adaptive management (Fig. 3). Designing and conducting research in collaboration with local land managers also is resulting in increased applicability of the research. Each study was conceived and implemented with land managers. During the course of data collection field tours to view experiments and field training sessions are conducted as an integral part of the regional research program.

Research results are often difficult to apply directly to large landscapes because managers do not always incorporate scale and the nested interaction of complex processes such as fire, herbivory, succession, land use change, or disturbance corridors into their activities. Researchers, on the other hand, do not usually integrate the routine operations of land managers, who are the end-users of invasive plant experiments, into their studies. The studies we present in our research framework were designed from the onset to incorporate the invasion process, scale, and land manager input. By using the adaptive management in our research framework (Fig. 2), we place research activities within a management context, and thereby avoid ineffectual approaches and overcome manager criticisms.

Conclusions

There are many plant species present east of the Cascade Mountains in the Pacific Northwest, as indicated in Table 1. Each of these species can be of concern to local land managers in the Blue Mountains Ecoregion. Hobbs and Humphries [30] suggest an approach to set priorities for management of invasive plants based on land value and the degree of disturbance or risk of invasion (Fig. 6). However, most extensive land management areas represent locations where determining management priorities is much more difficult than the process indicated by Hobbs and Humphries [30]. Scientists can provide insight into the management priority setting process by providing information on the biology of invasive species, invasibility of habitats, and effectiveness of management tactics. We believe that a regional network of scientists and natural resource managers working together is most effective in determining what species to study and to diminish the impacts of invasive plants on extensive land management systems. Scientific and other forms of expertise from various sources can be coordinated to produce state-of-the-art knowledge about natural resource areas that are at-risk and the human uses and values associated with those areas.

Experiments, risk assessments of invasive species, and projections of species spread across susceptible landscapes after introduction help managers evaluate the consequences of management activities, including doing nothing. Combining information about multiple species also should result in a powerful database for land managers to decide what areas and species should receive par-

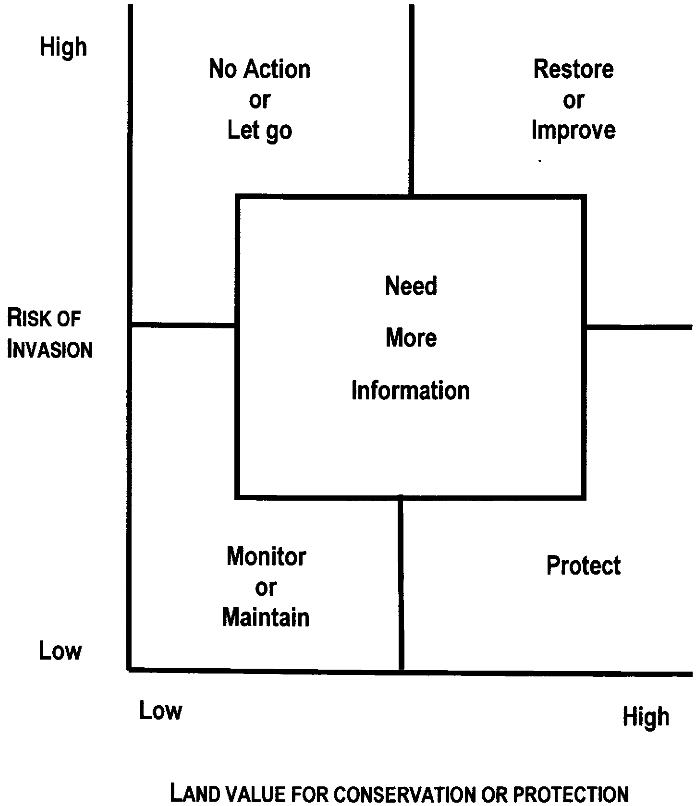

Figure 6. Assessment of management priorities for a region based on relative values of different sites for conservation and/or production, and their relative degree of risk to invasion. Modified from [25, 30].

ticular attention. Thus, scientifically rigorous and timely research is fundamental to a regional research framework (Fig. 2) for invasive plant management. Adaptive management (Fig. 3), where research results are continually brought forward and management practices are reassessed as new information becomes available, is a workable approach to integrate management and science to manage invasive plant species in extensive resource areas across a region [43].

Research can be advanced best with partnerships between scientists and land managers, where managers indicate crucial concerns and provide information about day-to-day management activities. Designing and conducting experiments in collaboration with local land managers can result in increased applicability of the research. A regional approach that places scientific study within a management context (Figs 2 and 6) can result in increased implementation of research results, continual adaptation of management plans and greater overall success in managing invasive plants.

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