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Flood and debris flow interactions with roads promote the invasion of exotic plants along steep mountain streams, western Oregon

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Abstract

This study examines the interactions among geomorphic and biogeographic processes that govern the invasion by two contrasting exotic plant species—a shrub, scotch broom (*Cytisus scoparius*) and an herb, foxglove (*Digitalis purpurea*), over several decades of road and stream networks in the H.J. Andrews Experimental Forest in western Oregon. Distributions of *C. scoparius* and *D. purpurea* were mapped along hillslopes and streams in 1993, 2002, and 2003. The mapped distributions were related to debris flow pathways and changes in stream morphology interpreted from field surveys and air photos over the period 1993 to 2003. Laboratory trials examined the response of seed germination to scarification (to test effects of transport by debris flows), soaking (to test effects of fluvial transport), and substrate texture (to test effects on establishment). *C. scoparius* and *D. purpurea* were present along roads and in clearcuts in the Andrews Forest from the 1970s to 2003, but invaded the stream (Lookout Creek) only after debris flows and floods during an extreme storm in 1996. Laboratory trials demonstrated that seeds could germinate on a variety of substrates after scarification and flood transport. Mapping and air photo/GIS analysis indicated that the distributions of exotic plants were located on freshly scoured bars and floodplains adjacent to the active channel, downstream of seed sources along roads that were connected to the main stem of Lookout Creek by road ditch drainage systems, and debris flow paths. This paper outlines a conceptual model for the invasion of exotic plants, highlighting the connectivity between road and stream networks provided by geomorphic processes in steep forested landscapes.

Keywords: Hydrochory; Road network; Stream network; Fluvial transport; Scotch broom (*Cytisus scoparius*); Foxglove (*Digitalis purpurea*)

1. Introduction

The spread of invasive exotic species into pristine environments, such as old growth forests, involves the interaction of human activities with landscape features and the attributes of life history of invasive and native species. In steep forested landscapes, the road network is an anthropogenic vector for the invasion of exotic plants into the forested landscape. Road networks provide sources of exotic plant propagules, transport mechanisms via vehicle and foot traffic and wind and water flows, and persistent light gaps and frequently disturbed soils where populations of exotic plant may become established and contribute seed to localized seed banks in roadside ditches and road fill (Parendes, 1997). Propagules of invasive plants may be dispersed by wind or water along networks of roads in steep forested landscapes (Spies et al., 2002).

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The ability of various species to spread along road and stream networks depends on modes of dispersal and the requirements of germination (Parendes and Jones, 2000). Seed dispersal by water (hydrochory) enables riparian plants to spread along a stream (Johansson et al., 1996; Vogt et al., 2004). Observational and experimental studies indicate that the processes of seed and sediment transport are linked in fluvial systems (Goodson et al., 2003; Merritt and Wohl, 2002). Patterns of distribution of invasive hydrochorous exotic plants in stream systems may be predicted at the landscape scale by considering the distribution of source plants (Campbell et al., 2002). The resulting distributions of exotic plants, however, are also likely to be sensitive to the hydrologic regime (Tabacchi et al., 1998), including episodic flooding (Brown and Peet, 2003; Pearce and Smith, 2001).

Networks of forest roads interact with water and sediment flowpaths (Forman et al., 2003; Jones et al., 2000; Wemple et al., 1996). Roadside ditches carry channelized flow during peak discharge events; some of this flow directly reaches first- and second-order streams (Wemple and Jones, 2003; Wemple et al., 1996). In a steep forested landscape, debris slides and debris flows initiate from roads in near-ridge, midslope, and lower slope positions, have complex interactions with roads in various hillslope positions, and may produce a cascade of linked fluvial and mass movement geomorphic processes that eventually reach the valley floors (Nakamura et al., 2000). Roads and valley floors may be stopping points for the boulders and large wood entrained by debris slides and debris flows, but the less viscous portions of the flow, water and fine sediment, may continue much further through fluvial processes which entrain and erode the roadbed, road fill, and hillslope below the road (Wemple et al., 2001).

How do roads, stream networks, floods, and geomorphic processes interact over time to influence the distribution of exotic plants in a landscape? Wind and animal dispersal may occur along roads and streams and at junctions between them. In addition, three mechanisms involving flows of water and sediment may transfer exotic plants from terrestrial environments along roads to streams. These are: (1) fluvial transport of seeds in channelized flow along roadside ditches to stream channels or to gullies etched below culvert outlets that are connected to streams; (2) transport by debris flows that entrain road fill material containing seed banks of exotic plants and deposit the material in valley floors; and (3) hybrid debris flow and fluvial transport that occurs when a debris flow entrains exotic plant material, the debris flow is stopped at a road, but water and fine sediment from the debris flow are routed along roadside ditches, erode new channels or deepen pre-existing channels, and deposit propagules in the valley floor and active stream channel. Depending upon the attributes of life history, such as tolerance to immersion and abrasion, as well as substrate, drainage, and light requirements, different exotic plants may exploit these various mechanisms to reach streams from road networks. Also, fluvial transport is a chronic process that may occur frequently, whereas transport by debris flow and hybrid debris flow/fluvial transport requires extreme floods.

The history of geomorphic processes and exotic plants at the H.J. Andrews Experimental Forest over the past 50 years provides useful context for disentangling these mechanisms. In 1994, scotch broom (*Cytisus scoparius*) occurred along 11% and foxglove (*Digitalis purpurea*) occurred along 1% of the road network in the Andrews Forest (based on presence/absence in 0.16 km sample units), but neither species was detected along the stream network (Parendes, 1997). In 1996 the Lookout Creek basin experienced a flood of record that involved many debris slides, debris flows, and major changes in stream channels (Johnson et al., 2000; Nakamura et al., 2000; Swanson et al., 1998). These geomorphic features were surveyed and added to a 50-year inventory of floods and geomorphic processes (Snyder, 2000; Swanson and Dyrness, 1975; Wemple et al., 2001). By 2002, *C. scoparius* occurred along 13% of road length and *D. purpurea* occurred along 5% of the road length (K. Cilenti, unpublished data), and a few dozen *C. scoparius* and hundreds of *D. purpurea* plants were noted along Lookout Creek. This study used field survey, historical air photos, GIS, and experimental treatment of the seeds of exotic plants to investigate the interactions of floods and debris flows with sources, transport mechanisms, and establishment sites of invasive exotic plants (*C. scoparius* and *D. purpurea*) that integrate road and stream networks in a steep, forested landscape.

2. Methods

2.1. Study site

The Andrews Forest occupies the 64 km^2 drainage basin of Lookout Creek, roughly 50 km east of Eugene in the western Cascade Range of Oregon. Topography is deeply dissected, and elevation ranges from 415 to 1615 m. Climate is mild maritime with dry summers and wet winters. Maximum monthly temperature varies between 19 and 28 °C in July and August to between 2 and 5 °C in December and January; monthly minimum temperatures are typically between 8 and 10 °C in July and August and from −2 to 1 °C during December through March (Smith, 2002). Low-elevation annual precipitation averages 230 cm, falling mostly as rain between November and March. Average annual precipitation at higher elevations is more than 355 cm and a seasonal snowpack accumulates. Native vegetation is coniferous forest of Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) ranging from 80 to more than 500 years old. Mostly from 1950 to 1970, 25% of basin area was converted to young forest by clearcutting in 10–30 ha patches followed by prescribed fire, and a network of access roads was created (Jones and Grant, 1996). *D. purpurea* and *C. scoparius* were present in the Andrews Forest by 1971. *C. scoparius* occurred along sections of road, in harvest patches, and at a quarry; *D. purpurea* was first observed only in harvest patches (Franklin and Dyrness, 1971; J. Franklin, personal communication, 2002).

Lookout Creek, a fifth-order stream draining the Andrews Forest, contains a network of over 138 km of streams. Stream environments range from high-gradient bedrock channels to wide alluvial stretches formed upstream from valley floor constrictions (Grant and Swanson, 1995). Much of the stream network consists of boulder-dominated, stepped-bed channel reaches with alternating pools and steep units (Grant et al., 1990). Lookout Creek has two major tributaries, Mack Creek (third-order) and McRae Creek (fourth-order). The road network in the Andrews Forest was constructed mainly during the 1950s and 1960s and consists of 119 km of roads, all of which are gravel except for 3 km of paved road along lower Lookout Creek at the entrance of the Andrews Forest (Wemple et al., 1996).

In February 1996 the Lookout Creek basin experienced an extreme rain-on-snow storm that delivered 330 mm of precipitation at low elevations and nearly 450 mm at high elevations over a 5-day period, with a daily maximum of >140 mm. Precipitation and warm winds melted snowpacks and produced a flood with an instantaneous peak discharge at Lookout Creek that was nearly four times the average annual peak discharge for the period 1950 to 2001 and the largest since gauging started in 1950 (Fig. 1). The storm triggered widespread change in the landscape (Swanson et al., 1998), with documented runoff along road networks (Wemple and Jones, 2003) and debris slides and flows from roads and tributary channels reaching the mainstem of Lookout Creek (Wemple et al., 2001). Several dozen debris flows scoured long stretches of the stream network (Snyder, 2000) and high-energy floodwaters reworked and altered channel morphology (Faustini and Jones, 2003;

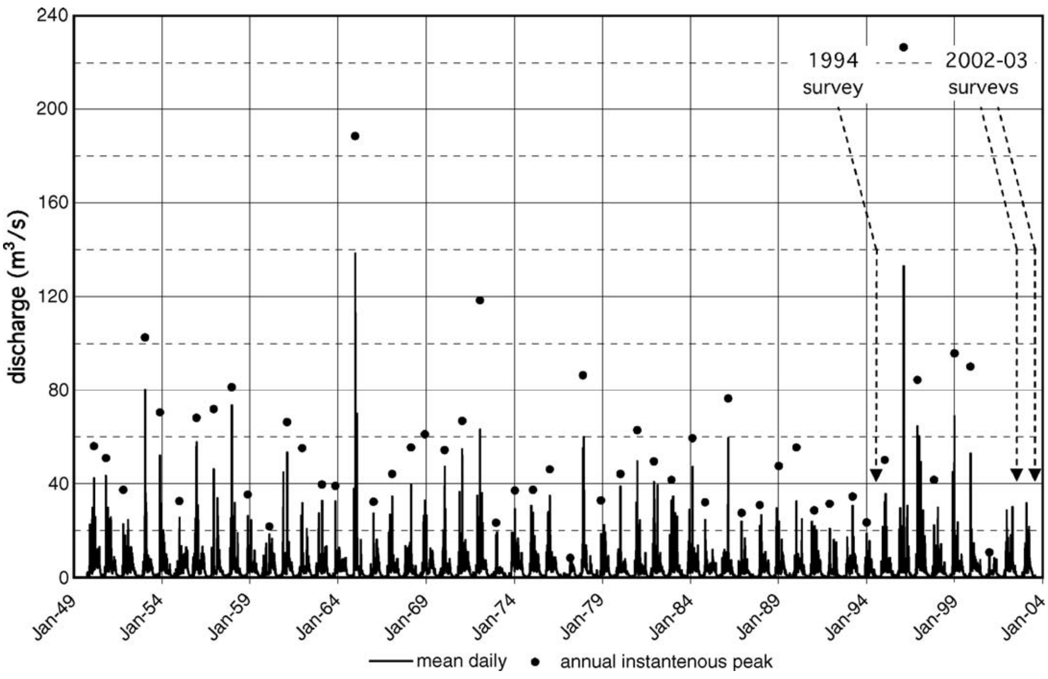

Fig. 1. Historical discharge at lower gauging station on Lookout Creek (USGS/USFS).

Wondzell and Swanson, 1999) and removed riparian vegetation (Johnson et al., 2000) in mainstem reaches of Lookout Creek and McRae Creek. Channel reworking continued with large storms in 1997, 1999, and 2000 that further reworked sediment delivered to channels from the 1996 event. These storms had a 5-day precipitation total of 270, 330, and 270 mm and daily maximum precipitation of 133, 145 and 167 mm at low elevation, respectively. These rainfalls produced peak discharges of 1.5 to 1.7 times the average annual peak discharge at Lookout Creek. Between 1996 and 2000, Lookout Creek experienced four of the eight largest annual peak flows in the period 1950–2003 (Fig. 1).

2.2. Ecology of target species

2.2.1. C. scoparius

C. scoparius, a leguminous perennial shrub (see photograph in Fig. 2a) in the Fabaceae family, is native to Europe. It was first introduced to the Pacific Northwest in the mid-1800s as an ornamental plant and later planted in areas to stabilize soil and control erosion (Gilkey, 1957; Pojar and MacKinnon, 1994). *C. scoparius* is now present in 25 states and is listed as a noxious weed in five states (USDA, 2004). It is an aggressive colonizer of disturbed habitats, such as logged areas, riverbeds, roadsides, and steep slopes (Bossard, 1991; Williams, 1981). Plants typically live for 10 to 12 years in the native environment (Waloff and Richards, 1977), although they can survive for as many as 23 years in exotic habitats (Smith and Harlen, 1991). *C. scoparius* is tolerant of a wide range of soil conditions but favors dry, sandy soils in full sunlight; it usually reaches 1 to 2 m, but can grow to be 4 m tall (Gill and Pogge, 1974). Plants can flower and set seed as early as the second year after germination, although most plants first reproduce in the third or fourth year (Smith and Harlen, 1991; Williams, 1981).

Each mature plant produces tens of thousands of seeds each year (Waloff and Richards, 1977) with high seed viability (Bossard, 1993). *C. scoparius* seeds are relatively large, generally about 3 mm in length with a mean mass of between 5 and 10 mg (Buckley et al., 2003; Gill and Pogge, 1974). Ripe seedpods open explosively, dispersing most seeds within 1 m of the parent plant (Smith and Harlen, 1991). Because of its high seed mass, *C. scoparius* seeds are not likely to be dispersed long distances by wind. Ants can disperse these seeds locally (<5 m), but animals are not effective long distance dispersers of *C. scoparius* seed (Bossard, 1991). Seeds are hard-coated and can remain viable in the seed bank for many years to decades (Bossard, 1993; Smith and Harlen, 1991). Common nursery practice involves propagation from cuttings (Wyman, 1986), but vegetative regeneration of *C. scoparius* from transported plant parts is not known to occur in natural environments.

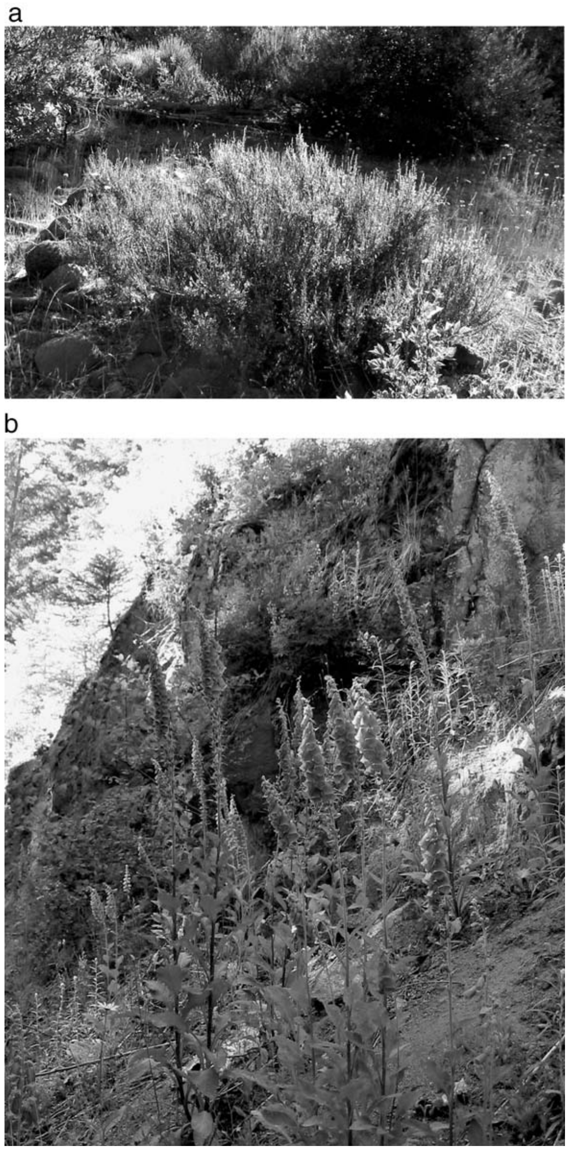

Fig. 2. Photographs of target species. (a) *Cytisus scoparius* shrub pictured in foreground and (b) erect stalks and bell-like flowers of *Digitalis purpurea*.

2.2.2. D. purpurea

D. purpurea, a short-lived perennial herb (see photograph in Fig. 2b) in the Scrophulariaceae family, is native to Europe (Silvertown, 1984; Sletvold, 2002). The plant, which was originally introduced to the Pacific Northwest for its ornamental appeal and medicinal properties (Dennis, 1980), is now common in fields and along roadways and forest margins (Pojar and MacKinnon, 1994) in 21 states (USDA, 2004) and is capable of rapidly spreading, crowding out native vegetation (Dennis, 1980). *D. purpurea* is able to germinate and establish early in disturbed habitat (Harper, 1977; Salisbury, 1942), and it particularly favors high light, high temperatures, and moderate levels of soil moisture (Salisbury, 1942; van Baalen, 1982). Plants usually produce an erect, flowering stem of up to 1.8 m tall (Pojar and MacKinnon, 1994) during the second summer, but can delay fruiting for several years (Salisbury, 1942; van Baalen and Prins, 1983).

D. purpurea is typically monocarpic, dying after fruit production, and an individual plant may produce tens or hundreds of thousands of seeds; however, plants have also been known to survive flowering (Salisbury, 1942; Sletvold, 2002). *D. purpurea* seeds are small and light, measuring 0.2 to 0.5 mm in length and weighing from 0.08 to 0.09 mg (Salisbury, 1942; Sletvold, 2002). Seeds are passively dispersed from the parent, over distances of up to 4 m (Hanson, 2000), and they can remain viable in the seed bank for years (van Baalen, 1982). *D. purpurea* is not known to reproduce vegetatively from transported plant parts.

2.3. Field surveys and mapping

Between July 1 and July 14, 2003, all third-, fourth-, and fifth-order streams (a total of approximately 24 km of streams) in the Andrews Forest were surveyed for *C. scoparius* and *D. purpurea.* Lower-order streams were not surveyed in this study because low light levels and less disturbed conditions had been linked to low or no densities of exotic plants (Parendes and Jones, 2000). Also in July 2003, 48.1 km of roads in the vicinity of, or directly crossing, third- or higher-order streams were surveyed to record the locations of *C. scoparius* and *D. purpurea*. This road survey was designed to supplement a comprehensive survey of the road network conducted in 2002 by K. Cilenti (unpublished data). Locations of exotic plants were delineated by GPS where possible. Approximate counts of the populations, substrate texture, light levels, and other site characteristics were documented and potential mechanisms for dispersal to and from the area were described. Sites of exotic plants along the stream were sketched and photographed, and distances were measured to active channel margins, riparian forest, secondary channels, bars, terrace or floodplain margins, or large wood.

2.4. Experimental treatments of seeds with water and sediment

Greenhouse and growth chamber experiments were conducted to determine the effects of (1) abrasion during tumbling with sediment and water, and (2) substrate texture on germination of seeds of *C. scoparius* and *D. purpurea.* Flotation trials were conducted to evaluate the floating ability of both species of seeds. Treatments were applied to commercially obtained seeds of *C. scoparius* (Carter Seeds, Vista, California) and *D. purpurea* (Ed Hume Seeds, Inc., Puyallup, Washington). Because seeds were not from local sources, and may have been subjected to treatments by the seed suppliers, the results of the germination experiments provide relative, but not absolute indications of treatment effects and are valid in a general qualitative sense. Sediment used in experiments was oven-dried at 121 °C for 2.5 h, dry-sieved and divided into 12 grain-size categories following American Society of Civil Engineers (ASCE) classification.

Viability and germination of seeds were determined separately. Seed viability was determined for two replicates of *C. scoparius* seeds ($n=95$ each) and two replicates of *D. purpurea* seeds ($n=102$ and 97) using the tetrazolium chloride method at the Oregon State University Seed Laboratory.

Germination trials tested the effects of (1) abrasion by tumbling and (2) substrate texture. Controls for germination trials involving *C. scoparius* consisted of five sets of 100 seeds: two replicate samples of untreated seeds, one “optimally” treated sample of seeds soaked for 2 h in 55 °C streamwater, one sample of seeds that floated in water but which received no treatment, and one sample of seeds that sank but which received no treatment. Control groups for *D. purpurea* included two replicate samples of untreated seeds and two samples of *D. purpurea* germinated for seed recovery correction trials (described below).

The effect of abrasion on seed germination was tested using 18 scarification (tumbling) treatments. Samples of 100 *C. scoparius* and *D. purpurea* seeds were combined with various sediment and streamwater mixtures and subjected to treatments ranging from 100 to 2000 rotations in a manually cranked tumbler (Watterson, 2004). All seeds that were recovered from sediment–water mixtures after tumbling were germinated on moist blotter paper under controlled conditions of 20 °C with 8 h light and 16 h dark at the Oregon State University Seed Laboratory. For *D. purpurea* germination trials following tumbling with sediment, correction factors were developed to account for losses of seeds incurred during the process of retrieval of seeds from sediment–water mixtures (Watterson, 2004). The effect of the texture of the substrate on germination was tested by planting two replicate samples of 25 "optimally" treated seeds for each species, selected randomly from the same seed lots as the tumbling experiment, in uniformly textured substrates ranging from very coarse gravel to fine sand, as well as some heterogeneous textures (Watterson, 2004).

Germination trials for controls and tumbling treatments were conducted from August 26, 2003 to October 15, 2003 (for *D. purpurea*) or February 6, 2004 (for *C. scoparius*); germination trials in substrates were conducted from August 24, 2003 to September 27, 2003 (for *D. purpurea*) or February 6, 2004 (for *C. scoparius*). Samples (blotter papers or pots) were examined and germinated seeds were counted and removed at approximately 3-day intervals for the first 2 months and at 1-week intervals thereafter. Trials were terminated when no new germination occurred for 2 weeks (Watterson, 2004).

The lengths of time seeds could float was determined by separately placing 10 replicates each of *C. scoparius* and *D. purpurea* seeds ($n=25$) in 20 glass containers filled with 150 ml of Corvallis, Oregon tap water over the period from January 23 and February 7, 2004. The floating status of the seeds was recorded at 12-h intervals after vigorously disturbing the containers to disperse adhered seeds and break the surface tension of the water.

2.5. GIS and aerial photograph-based analyses

Occurrences of exotic plants along the streams were mapped and combined into discrete patches and included in a GIS for analysis. *C. scoparius* plants, located more than 10 m from other *C. scoparius* individuals, were assigned to separate patches. Because of greater distances of dispersal by wind, *D. purpurea* plants spaced more than 25 m apart were assigned to different patches. The GIS was created in ArcGIS (ESRI, Redlands, CA) and included (1) a 10-m digital elevation model (DEM); (2) spatial layers of the Andrews Forest boundary, road network, hydrography, and historical forest harvesting activities; (3) occurrences of *C. scoparius* and *D. purpurea* at 0.16 km intervals along the road network from Parendes (1997, unpublished data) and K. Cilenti (unpublished data); and (4) paths of debris flows occurring between 1946 and 1996 (K. Snyder, unpublished data). For finer spatial analysis of changes in selected reaches of streams, USDA Forest Service (USFS) color aerial photographs (September 1990 and September 1996) and USDI Geological Survey (USGS) digital orthophoto quadrangles (September 2000) were scanned, georeferenced, and overlain in the GIS.

The GIS was sampled to create (1) cross-sectional profiles of valley shape at 31 transects spaced at roughly 350 m intervals throughout the portion of Lookout Creek containing *C. scoparius* and *D. purpurea*; (2) a longitudinal profile from which stream gradients were calculated for the 32 segments between these transects; and (3) estimates of the width of the unvegetated floodplain at the 31 transect locations based on interpretation of aerial photographs of 1994, 1996, and 2000.

3. Results

By 2003, despite some manual removal and cutting of roadside populations, *C. scoparius* populations consisted of hundreds of individuals distributed along 10–15% of the road network length and in several clearcuts, and 25 plants occurred in eight patches in Lookout Creek. By 2003, *D. purpurea* populations consisted of thousands to tens of thousands of individuals along nearly 6% of the road length and in at least two clearcuts, and roughly 540 individual plants were distributed in 49 patches along 1.3 km of stream network (Watterson, 2004). Forested areas have not been searched thoroughly, but no populations of *C. scoparius* or *D. purpurea* have been observed in forests.

3.1. Sources of exotic plants in the landscape: clearcuts and roads connected to streams

A number of potential sources of seeds for populations of *C. scoparius* in Lookout Creek existed prior to the flood of 1996: along roads in lower hillslope positions north and south of Lookout Creek and west of McRae Creek, along midslope roads northwest of the junction of Lookout and McRae Creeks, and in a 1988 clearcut upslope of the road (Fig. 3a,b). During the flood in early February 1996, one debris flow initiated in the clearcut above the road and left a deposit on the road and against the trees on the fillslope below the road (center of Fig. 3a,b). A second debris flow initiated from a roadfill on a midslope road northwest of the junction of McRae and Lookout Creeks, and deposited on the road (upper center of Fig. 3a,b). Because the culvert was blocked, fine sediment and water from this debris flow deposit continued downslope along the inboard roadside ditch and across the road. In both cases, *C. scoparius*

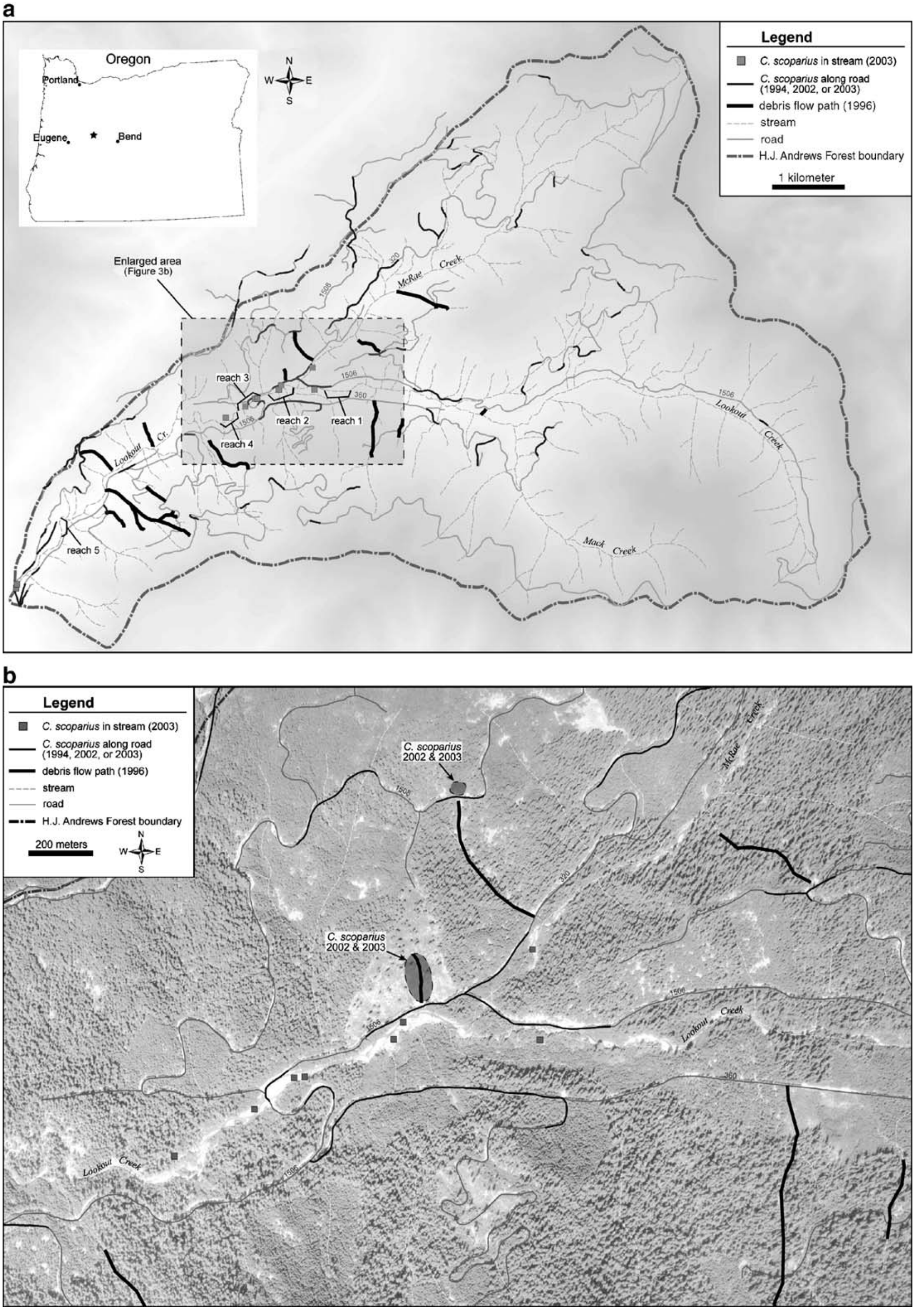

Fig. 3. (a) Map of the distribution of *Cytisus scoparius* along roads and streams in the Andrews Forest since 1994 with 1996 geomorphic disturbances. Figure shows the results of road and stream surveys in 2003 combined with results from road surveys conducted in 1994 (L. Parendes, unpublished data) and 2002 (K. Cilenti, unpublished data) and paths of debris flows from 1996 (K. Snyder, unpublished data). (b) Enlarged view of the distribution

seeds entrained by the debris flows or extreme water flows occurring in flowpaths created by diversions and blockages caused by debris flow deposits may have been carried in these fine sediment-laden waters into McRae and Lookout creeks. Seven of the eight patches of *C. scoparius* in Lookout Creek are just downstream from these entry points. The eighth patch of *C. scoparius* in Lookout Creek occurs just downslope from a portion of the road where *C. scoparius* has been present since at least 1994.

Potential sources of seeds for *D. purpurea* populations in Lookout Creek occur along roads or in clearcuts upslope and upstream. Prior to the flood of 1996, *D. purpurea* had been present along an east–west oriented midslope road just south of Lookout Creek (lower center and right of Fig. 4a,b). By 2003 *D. purpurea* was very abundant along much of that road and in two adjacent harvest patches created in 1985. During the flood of early February 1996, two debris flows originated in forest and in roadfill on an upslope portion of the road on the north-facing slope south of Lookout Creek and ran along a clearcut where *D. purpurea* was present, stopping at the lower road where *D. purpurea* was documented in 1994 (lower center of Fig. 4a,b). Because the culvert was blocked, fine sediment and water from this debris flow deposit continued downslope along the inboard roadside ditch and across the road, and entered a small (<2 m wide) channel to the west, where it eroded a gully 2 m deep downslope to the valley floor of Lookout Creek. *D. purpurea* seeds entrained by the debris flow or by flow in ditches may have passed in this manner into Lookout Creek, which is >150 m downslope from the road. All but one of the *D. purpurea* patches in 2003 were downstream of the confluence of this tributary with the Lookout Creek mainstem channel. The clearcut and road south of Lookout Creek and east of Mack Creek (lower right of Fig. 4a,b) are a second potential source of seed for *D. purpurea* in Lookout Creek. During the flood of 1996, seeds of *D. purpurea* may have been transported in channelized flow along roadside ditches lining this road, which eventually contributes to a tributary channel that enters Lookout Creek approximately 350 m upstream of where *D. purpurea* occurred in Lookout Creek in 2003 (Fig. 5a,b).

3.2. Transport mechanisms for exotic plant seeds

Seeds of *C. scoparius* and *D. purpurea* can float, survive transport by water and abrasion, and germinate on fine- and coarse-textured substrates typical of channel bars and banks in Lookout Creek, but the two species differ in responses to immersion and abrasion. Experimental trials indicated that germination of *C. scoparius* seeds was less adversely affected by abrasion from tumbling with sediment than that of *D. purpurea* seeds, but germination of *D. purpurea* seeds was little affected by prolonged flotation, sinking, or tumbling in water. Prior to treatments, the viability of *C. scoparius* seeds used in this study was very high (99%, determined by tetrazolium chloride testing), whereas seed germination was only 74% after the "optimal" treatment (submergence in 55 °C water for 2 h before planting on blotter paper) and 43% for untreated seeds, irrespective of whether seeds floated or sank (Table 1). Prior to treatment, viability of *D. purpurea* seeds used in this study was <70%, and seed germination averaged 73% after the "optimal" treatment (which was no treatment) (Table 1).

In scarification trials, germination of both *C. scoparius* and *D. purpurea* was reduced by tumbling with sediment, especially very coarse sand and fine gravel, or sediment–water mixtures compared to tumbling with water only, but as much as one-third of seeds germinated after most scarification treatments (Table 1). Germination of *C. scoparius* was not consistently affected by the duration of scarification or the texture (i.e., coarseness) of the scarification mixture used in tumbling treatments, but germination of *D. purpurea* declined with longer scarification treatments and finer textured scarification mixtures (Table 1). In flotation trials, *D. purpurea* seeds were capable of floating for many hours and could germinate while floating and after sinking, whereas very few *C. scoparius* seeds floated, and only for a few hours, and submerged seeds became moldy during the trials (Watterson, 2004).

3.3. Channel morphology and patches of exotic plants in streams

Local features, such as boulder berms and wood, reach-scale stream gradient, and the widths of the active floodplain and valley floor were all related to the distribution of *C. scoparius* and *D. purpurea* patches in Lookout Creek in 2003. In 2003, many patches of *C. scoparius* and *D. purpurea* in Lookout Creek were located on elevated cobble bars or terraces, often in settings locally protected from flood scour by large wood or boulder berms. Exotic plants were established in hydraulic refuges, such as spaces between cobbles or in patches of fine sediment downstream from obstructions. In experimental trials, rates of germination of *C. scoparius* were high (80%

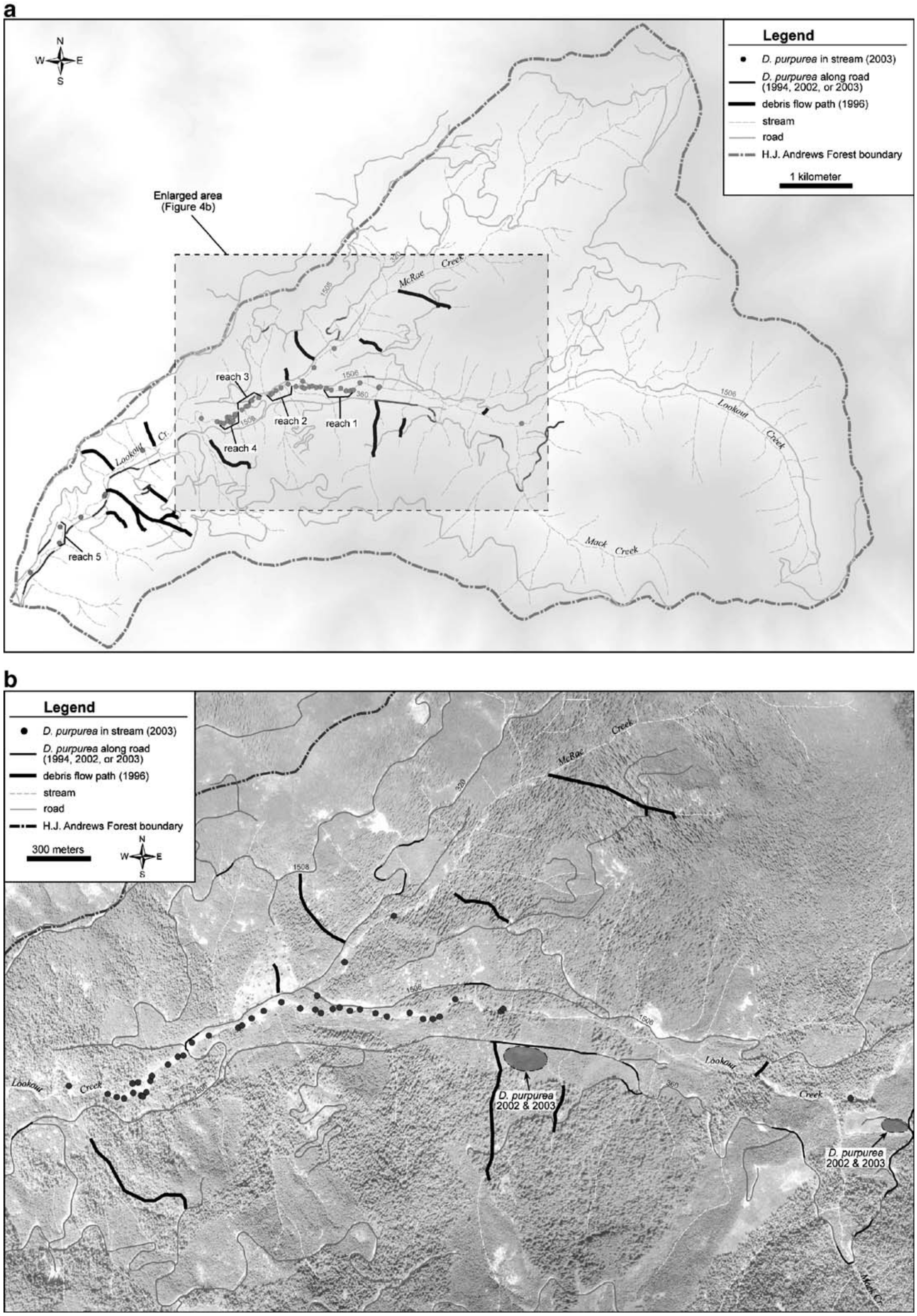

Fig. 4. (a) Map of the distribution of *Digitalis purpurea* along roads and streams in the Andrews Forest since 1994 with 1996 geomorphic disturbances. Figure shows the results of road and stream surveys in 2003 with results from road survey conducted in 1994 (Parendes, unpublished data) and 2002 (Cilenti, unpublished data) and debris flow paths from 1996 (Snyder, unpublished data). (b) Enlarged view of the distribution of *D. purpurea* in the vicinity of the junction of McRae–Lookout creeks since 1994.

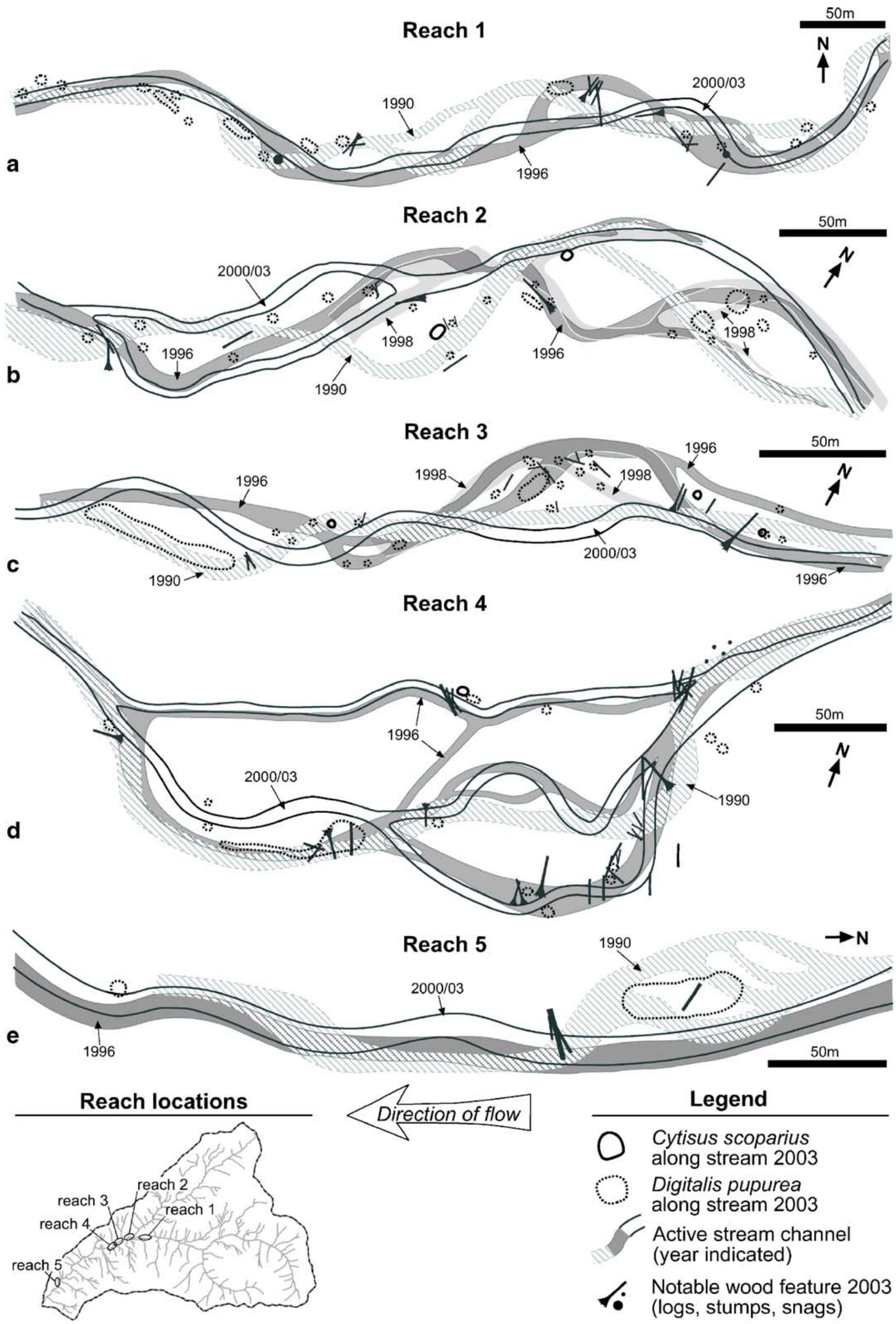

Fig. 5. Mapped locations of patches of *Cytisus scoparius* and *Digitalis purpurea* relative to the positions of the stream channel within the valley floor of Lookout Creek. Positions of the low-flow channel in 1990 to 2000 were mapped from aerial photography with additional channel interpretations from Nakamura and Swanson (1993), Wondzell and Swanson (1999), and Faustini (2000). Positions of the low-flow channel in 2003 were constructed using field observation. Positions include (1) the active low-flow channel in 1990 that was abandoned during the flood of February 1996, (2) the active low-flow channel in summer of 1996 (post-flood), (3) the active low-flow channel in 1998 after channel migration during floods of 1997, (4) the active low-flow channel in 2000 to 2003 after channel migration during floods of 1999, and (5) channel bars and margins. Vegetation patches and notable wood features were mapped in the summer of 2003 using field observation and GPS.

Table 1
Percents of germination from experimental trials of *Cytisus scoparius* and *Digitalis purpurea* seeds designed to simulate conditions to which seeds may be exposed during transport by floodwaters and/or debris flows

Treatment type	Tumbling details		Scarification mixture composition			Range of germination (%)	Average germination (%)	Average change from control
	Rotations	Duration (min)	Mixture type [a]	Sediment (%)	Water (%)			
Cytisus scoparius scarification trials (seed viability = 99%)								
Control	–	–	–	–	–	32–54	43 (±22)	–
Optimal	–	–	–	–	–	74	74	+31
Floats	–	–	–	–	–	40	40	−3
Sinks	–	–	–	–	–	30	30	−13
Tumbled	100	2	V.c. sand–fine gravel	25–100	0–75	16–62	40	−3
Tumbled	100	2	Water	0	100	30	30	−13
Tumbled	500	10	V.c. sand–fine gravel	50	50	28–40	34	−9
Tumbled	1000	20	V.c. sand–fine gravel	25–100	0–75	28–42	36	−7
Tumbled	1000	20	Water	0	100	42	42	−1
Tumbled	2000	40	V.c. sand–fine gravel	50	50	18–38	28	−15
Digitalis purpurea scrarification trails (seed viability ≤ 70%)								
Control	–	–	–	–	–	71–75	73 (±4)	–
Tumbled	100	2	V.c. sand–fine gravel	25–100	0–75	10–59 [b]	49 [b]	−24
Tumbled	100	2	Water	0	100	63	63	−10
Tumbled	500	10	V.c. sand–fine gravel	50	50	24–26 [b]	25 [b]	−48
Tumbled	1000	20	V.c. sand–fine gravel	25–100	0–75	2–63 [b]	43 [b]	−30
Tumbled	1000	20	Water	0	100	81	81	+8
Tumbled	2000	40	V.c. sand–fine gravel	50	50	0–57 [b]	29 [b]	−44

Treatments involved various durations of tumbling to scarify seeds, including varying mixtures of sediment textures and sediment–water ratios. Sizes of seed samples precluded replication of treatments, and seeds were purchased commercially, so only ranges of germination are shown, without standard deviations. See text for further details.
Germination conditions: moist blotter papers, 8 h/day artificial light, temperature 20 °C.
[a] Sediment classification based on American Society of Civil Engineers (ASCE) and National Research Council Standards.
[b] Germination corrected for seed loss in cured during seed recovery after tumbling treatments. Correction factor equals average germination of *D. purpurea* control samples (73%) divided by germination for the relevant *D. purpurea* correction trial (v.c. sand: 37%, fine gravel: 42.5%, v.c. sand/fine gravel mixtures: 39.75%).

to 90%) in all but the extremely coarse and fine types of substrate, whereas rates of germination of *D. purpurea* were highest (36%) in moderately coarse substrates (Table 2).

At the reach scale, patches of plants were mostly located on bars and banks where flood scouring since 1990 had noticeably widened the unvegetated floodplain. Patches of exotic plants occurred where the 1996 flood had reactivated old secondary channels (Fig. 5, Table 3), the channel had migrated across a wide valley floor (Fig. 5b, center of Fig. 5c), or a secondary channel had been abandoned (Fig. 5b, lower left corner of Fig. 5c). In many cases, patches of *D. purpurea* appear to have become established in secondary channels that temporarily conveyed water during floods since 1996 or were abandoned during channel reworking since 1996 (Fig. 5b, Table 3). All patches of *C. scoparius* and *D. purpurea*, surveyed along streams in 2003, occurred either in locations previously occupied by active channels that were abandoned during the flood of 1996 or in subsequent floods of 1997 and 1999, or on channel bars and margins which were inundated during those high flows (Fig. 5, Table 3).

Patches of *C. scoparius* and *D. purpurea* along the stream in 2003 were more likely to be established in unconstrained, low-gradient reaches with wide valley floors. *C. scoparius* and *D. purpurea* often occupied stream reaches through wide valleys, most notably the middle reach of Lookout Creek where the channel is relatively unconstrained by valley shape, and valley width ranges from 60 to almost 170 m. *D. purpurea* were markedly less common, and *C. scoparius* did not occur downstream of a >1.1 km constrained reach (Fig. 6a,b) where the valley floor is pinched to an average width of 25 m (Grant and Swanson, 1995) by an impinging, slow-moving, deep landslide (Swanson and James, 1975).

C. scoparius was restricted to and *D. purpurea* was particularly frequent in low-gradient reaches of streams (Fig. 6a), excluding the roadside populations of *C. scoparius* at the mouth of Lookout Creek. *C. scoparius*

Table 2
Percents of germination from experimental trials of *Cytisus scoparius* and *Digitalis purpurea* seeds designed to simulate different substrate conditions present along streams

Substrate type	Substrate composition		Average germination (%)	
	Particle type[a]	% by volume	*C. scoparius* (viability = 99%)	*D. purpurea* (viability ≤ 70%)
Sand and gravel mix	Very coarse sand	70	82	4
	Medium gravel	30		
Coarse gravel	Coarse gravel	100	2	0
Medium gravel	Medium gravel	100	80	0
Very fine gravel	Very fine gravel	100	90	36
Coarse sand	Coarse sand	100	84	18
Medium sand	Medium sand	100	88	12
Fines	Fine sand	33	2	2
	Very fine sand	33		
	Silt and clay	33		

Seeds were purchased commercially, so only average germination rates are shown, without standard deviations.
Germination conditions: 10 to 40 h/day indirect natural light, temperature 15 to 34 °C.
[a] Sediment classification based on American Society of Civil Engineers (ASCE) and National Research Council standards.

occurred on average in one of every six sampled segments of the streams, but in one-half of sampled segments with gradients between 1% and 3%. *D. purpurea* occurred in one-half of sampled segments of streams, but in three of four segments with gradients below 1%. In summer 2003 *C. scoparius* and *D. purpurea* were more frequent in the reaches of streams where the unvegetated floodplain had been widened by the flood of 1996 and which remained widened (Fig. 6b). Widths of the unvegetated floodplain in 1996 and 2000 were roughly inversely related to stream gradients (Fig. 6a,b).

Table 3
Frequency of patches of *Cytisus scoparius* and *Digitalis purpurea* by location relative to the positions of the stream channel within the valley floor of Lookout Creek (Fig. 4)

Species, reach	1990	1996	1998	2000/03		Total
				Bar	Margin	
C. scoparius						0
Reach 1						0
Reach 2					2	2
Reach 3	2				1	3
Reach 4					1	1
Reach 5						0
Total	2	0	0	0	4	6
D. purpurea						
Reach 1	7	4			6	17
Reach 2	4	3	6	2	6	21
Reach 3	5*	6	5		5	21
Reach 4	2	4*		3	5	14
Reach 5	1*				1	2
Total	19	17	11	5	23	75

Positions include (1) the active channel in 1990 that was abandoned during the flood of February 1996, (2) the active channel in August 1996 (post-flood), (3) the active channel in 1998 after channel migration during floods of 1997 (position only available for portions of reaches 2 and 3), and (4) bars and margins relative to the position of the active channel in 2000 to 2003 after migration during floods of 1999. Patches that spanned more than one position were assigned to the position in which the largest fraction of the patch was located and the most recent time of channel occupation. Locations of the three very large patches of *D. purpurea* are indicated by asterisks (*).

4. Discussion

C. scoparius and *D. purpurea* were present along roads and in clearcuts in the Andrews Forest from the 1970s to 2003, but appear to have invaded the stream network only after geomorphic processes in 1996 overcame barriers to stream invasion. Fluvial processes, debris flows, and hybrid debris flow/fluvial process mechanisms associated with the 1996 flood (Fig. 7) overcame barriers to seed dispersal by transporting seeds into the mainstem of Lookout Creek from hillslope source locations along roads and in clearcut patches. Furthermore, geomorphic processes, acting along the mainstem of Lookout Creek, created suitable conditions for seed deposition, germination, and establishment by removing vegetation and creating sites protected from scour. Seeds were probably deposited in hydraulic refuges protected from scour such as on boulder berms, near large wood or in secondary channels, most likely in middle reaches of the stream network where the unvegetated floodplain was widest and where stream gradient was lowest. The removal of vegetation in the floodplain created locally higher light levels along parts of the stream corridor, and possibly increased daytime temperatures at the ground surface, conditions that have been shown to increase seed germination in *C. scoparius* and *D. purpurea*

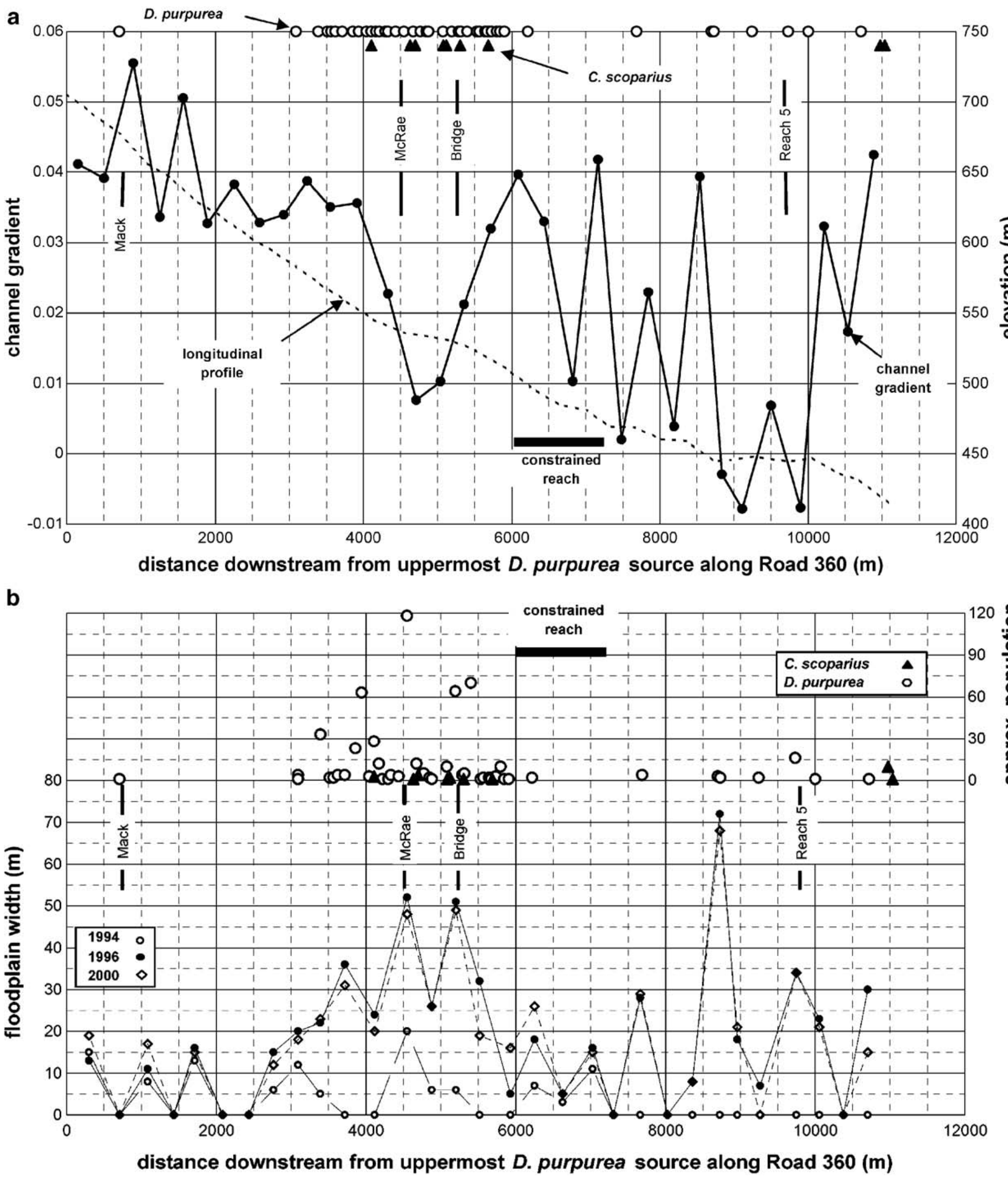

Fig. 6. Aspects of channel and valley floors along Lookout Creek in relation to the distributions of *Cytisus scoparius* and *Digitalis purpurea*. (a) Stream gradient (primary *y*-axis) in Lookout Creek and the longitudinal stream profile (secondary *y*-axis) (derived from a 10-m DEM) as a function of distance downstream of the uppermost source of seeds of *D. purpurea*. Note the location of a >1100 m constrained reach as mapped by Grant and Swanson (1995) where a deep-seated earthflow has impinged the valley floor. (b) Widths of the unvegetated floodplain measured from aerial photographs of 1994, 1996, and 2000 (primary *y*-axis) and approximate populations of *C. scoparius* and *D. purpurea* observed in streams in 2003 (secondary *y*-axis) as a function of distance downstream of the uppermost source of seeds of *D. purpurea*.

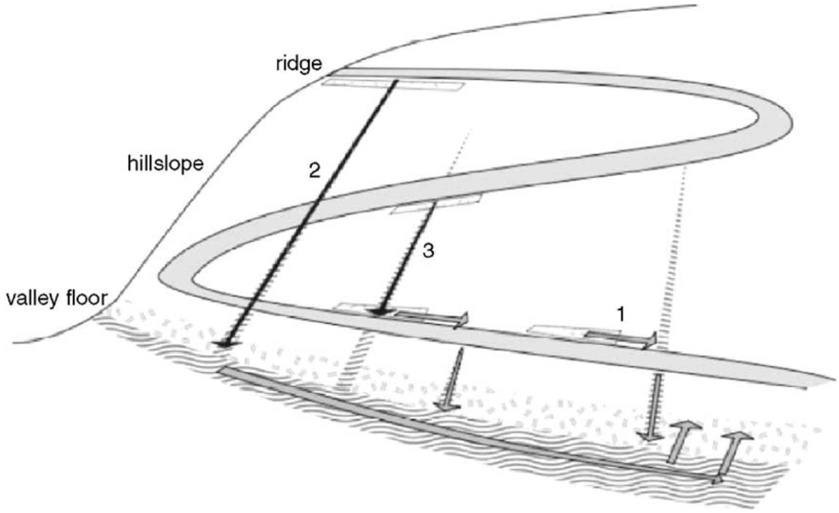

Fig. 7. Three mechanisms for invasion of exotic plants (confetti pattern) established along roads (double lines) to streams (wave pattern) and riparian areas (bird's foot pattern) by hydro-geomorphic processes in a steep forested landscape. Mechanisms are fluvial transport (grey arrows), debris flow transport (dark grey arrows), or hybrid debris flow and fluvial transport. Exotic plant propagules dispersed locally (confetti pattern) may be (1) entrained by overland flow in a ditch whose flow contributes to a stream, or to a culvert with a gully eroded below its outfall that connects to a stream; (2) entrained by a debris flow which deposits on the valley floor; or (3) entrained by a debris flow that stops at a road, plugging a culvert and diverting water and fine sediment down the roadside ditch to another channel which connects to the valley floor.

(Bossard, 1993; McAlpine and Drake, 2002; Tarrega et al., 1992; van Baalen, 1982).

Once *C. scoparius* and *D. purpurea* had become established along the mainstem stream, subsequent floods may have facilitated redistribution of *C. scoparius* and *D. purpurea* within the stream network. Allowing 2 years for plants to reach reproductive maturity, by 1998 patches of *C. scoparius* and *D. purpurea* that had been established in 1996 along active and secondary channels and on bars and terraces in lower McRae Creek and in middle Lookout Creek could become sources for down-gradient seed transport during the floods in 1999, possibly producing additional generations of patches that were sampled in 2003. Almost one-third of *D. purpurea* patches along the stream in 2003 were located in active channels created during the February 1996 flood, that were subsequently abandoned during floods of late 1996 and 1999 (Fig. 5, Table 3).

The 1996 flood involved an unprecedented interaction between the road network and the stream network in this basin. For the interaction to occur, the flood had to be sufficiently large to generate debris slides and road-related erosion, and exotic species had to be sufficiently widespread on roads to be entrained by episodic floods or debris slides. These conditions were met in 1996, by which time *D. purpurea* and *C. scoparius* had come to occupy roughly 10% of the road network length (Parendes, 1997; S. Sheehy, unpublished data). In 1996, numerous debris slides originated in road fill and some originated in clearcuts; many of these entrained additional material when they passed roads lower on the hillslope, and the character of these "disturbance cascades" became more fluid at lower hillslope positions (Wemple et al., 2001; Nakamura et al., 2000). Although earlier extreme floods in this basin (in 1964 and 1972, Fig. 1) generated debris slides and road erosion, *C. scoparius* and *D. purpurea* were either absent, or too sparsely distributed to be introduced into the stream.

Differences in the life histories between *C. scoparius* and *D. purpurea* produced contrasting interactions with geomorphic processes (Fig. 7). *D. purpurea* seeds may have been transported by fluvial or hybrid debris flow/fluvial transport because greater abundance, small size, and capacity to float after germination facilitate entrainment and transport during relatively minor flows. The location of *D. purpurea* plants in patches of fine sediment on active channel margins indicates that minor flows rather than major flows are involved in the redistribution of *D. purpurea* within the stream. In combination with the faster time of *D. purpurea* to reproductive maturity compared to that of *C. scoparius*, these factors may account for the greater downstream expansion of *D. purpurea* compared to *C. scoparius* in Lookout Creek. In contrast, the pollination requirements for reproduction in *C. scoparius* (Parker, 1997) may delay the production of seed by plants established along the stream, whereas the relative inability of the seeds to float may make *C. scoparius* dependent upon larger flows for seed transport in streams. Thus, opportunities for expansion of *C. scoparius* into and along a stream may be limited to large peak discharges, which provide high-energy, sediment-rich flows suitable for entrainment, scarification, and deposition of *C. scoparius* seeds. The location of *C. scoparius* plants on coarse-textured high bars or banks where subsequent inundation is unlikely indicate that relatively large floods are involved in spreading *C. scoparius* along the stream.

This case study of the Andrews Forest suggests that interactions among road and stream networks involving floods and debris flows may transport seeds across environmental barriers in many landscape settings. Geomorphologists and plant ecologists have begun to examine the role of floods for seed transport (e.g., Goodson et al., 2003; Merritt and Wohl, 2002; Vogt et al., 2004). Geomorphic studies of flood effects on stream channels have focused on the energetics of debris flows and associated large structural elements of stream channels (e.g., Benda et al., 2004). An important ecological story occurs in the low-viscosity tails of debris flows and diverted runoff created by debris flow blockage of road drainage systems, which may travel farther than the bouldery, wood-rich snouts, and by transporting exotic plant propagules may produce a more extensive and persistent biological legacy in stream networks. To capture the phenomena documented in this study, landscape-scale models of invasion along streams (e.g., Campbell et al., 2002) need to incorporate road networks, road-stream network interactions, and the episodic, stochastic nature of floods and debris flows.

These spatial and temporal processes indicate that a wave of invasion does not pass uniformly through the landscape; instead exotic species spread along road networks, and thence to stream networks via geomorphic processes. In this study, *C. scoparius* and *D. purpurea* were dispersed up-gradient by traffic or other means along a distributing road network over a two-decade period lacking extreme floods, then reversed direction and followed gravitational flowpaths of water and debris slides down-gradient during subsequent floods. A similar invasion pattern of up-gradient introduction along roads with subsequent down-gradient transport via water has also been documented in the spread of pathogens across landscapes (Jules et al., 2002). Road intersections with stream channels, including those created by the road drainage system (Jones et al., 2000; Wemple and Jones, 2003), were key places in the landscape where expansion of exotic plants occurred.

Land managers and others seeking to control the spread of exotic plants in the landscape might focus their attention on these locations to reduce the chances of exotic plant spread into stream systems.

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References

Benda, L., Andras, K., Miller, D., Bigelow, P., 2004. Confluence effects in rivers: interactions of basin scale, network geometry, and disturbance regimes. Water Resources Research 40, W05402. doi:10.1029/2003WR002583.

Bossard, C.C., 1991. The role of habitat disturbance, seed predation, and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. American Midland Naturalist 126, 1–13.

Bossard, C.C., 1993. Seed germination in the exotic shrub *Cytisus scoparius* (scotch broom) in California. Madrono 40, 47–61.

Brown, R.L., Peet, R.K., 2003. Diversity and invasibility of southern Appalachian plan communities. Ecology 84, 32–39.

Buckley, Y.M., Downey, P., Fowler, S.V., Hill, R., Memmot, J., Norambuena, H., Pitcairn, M., Shaw, R., Sheppard, A.W., Winks, C., Wittenberg, R., Rees, M., 2003. Are invasives bigger? A global study of seed size variation in two invasive shrubs. Ecology 84, 1434–1440.

Campbell, G.S., Blackwell, P.G., Woodward, F.I., 2002. Can landscape-scale characteristics be used to predict plant invasions along rivers? Journal of Biogeography 29, 535–543.

Dennis, C.R.J., 1980. Gilkey's Weeds of the Pacific Northwest. Oregon State University Press, Corvallis, Oregon.

Faustini, J.M., 2000. Stream channel response to peak flows in a fifth-order mountain watershed. PhD dissertation, Oregon State University.

Faustini, J.M., Jones, J.A., 2003. Influence of large woody debris on channel morphology and dynamics in steep, boulder-rich mountain streams, western Cascades, Oregon. Geomorphology 1298, 1–19.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.

Franklin, J.F., Dyrness, C.T., 1971. A checklist of vascular plants on the H.J. Andrews Experimental Forest, western Oregon. Research note PNW-138. US Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Gilkey, H.M., 1957. Weeds of the Pacific Northwest. Oregon Press, Portland, Oregon.

Gill, J.D., Pogge, F.L., 1974. *Cytisus scoparius*, scotch broom. In: Schopmeyer, C.S. (Ed.), Seeds of Woody Plants in the United States. USDA Agricultural Handbook, vol. 450. USDA Forest Service, Washington, DC, pp. 370–371.

Goodson, J.M., Gurnell, A.M., Angold, P.G., Morrissey, I.P., 2003. Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the River Dove, Derbyshire, UK. River Research and Applications 19, 317–334.

Grant, G.E., Swanson, F.J., 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. In: Costa, J.E., Miller, A.J., Potter, K.W., Wilcock, P.R. (Eds.), Natural and Anthropogenic Influences in Fluvial Geomorphology. Geophysical Monograph, vol. 89. American Geophysical Union, Washington, DC, pp. 83–101.

Grant, G.E., Swanson, F.J., Wolman, M.G., 1990. Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. Geological Society of America Bulletin 102, 340–352.

Hanson, D.E., 2000. Population dynamics of three early seral herb species in Pacific Northwest forests. PhD dissertation, Oregon State University.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.

Johansson, M.E., Nilsson, C., Nilsson, E., 1996. Do rivers function as corridors for plant dispersal? Journal of Vegetation Science 7, 593–599.

Johnson, S.L., Swanson, F.J., Grant, G.E., Wondzell, S.M., 2000. Riparian forest disturbance by a mountain flood—the influence of floated wood. Hydrological Processes 14, 2683–2702.

Jones, J.A., Grant, G.E., 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. Water Resources Research 32, 959–974.

Jones, J.A., Swanson, F.J., Wemple, B.C., Snyder, K.U., 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14, 76–85.

Jules, E.S., Kauffman, M.J., Ritts, W.D., Carroll, A.L., 2002. Spread of and invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. Ecology 83, 3167–3181.

McAlpine, K.G., Drake, D.R., 2002. The effects of small-scale environmental heterogeneity on seed germination in experimental treefall gaps in New Zealand. Plant Ecology 165, 207–215.

Merritt, D.M., Wohl, E.E., 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. Ecological Applications 12, 1071–1087.

Nakamura, F., Swanson, F.J., 1993. Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surface Processes and Landforms 18, 43–61.

Nakamura, F., Swanson, F.J., Wondzell, S.M., 2000. Disturbance regimes of stream and riparian systems—a disturbance-cascade perspective. Hydrological Processes 14, 2849–2860.

Parendes, L.A., 1997. Spatial patterns of invasion by exotic plants in a forested landscape. PhD dissertation, Oregon State University.

Parendes, L.A., Jones, J.A., 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology 14, 64–75.

Parker, I.M., 1997. Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. Ecology 78, 1457–1470.

Pearce, C.M., Smith, D.G., 2001. Plains cottonwood's last stand: can it survive invasion of Russian Olive onto the Milk River, Montana Floodplain? Environmental Management 28, 623–637.

Pojar, J., MacKinnon, A., 1994. Plants of Coastal British Columbia. Lone Pine Publishing, Vancouver, B.C.

Salisbury, E.J., 1942. The Reproductive Capacity of Plants: Studies in Quantitative Biology. G. Bell and Sons, London.

Silvertown, J., 1984. Death of the elusive biennial. Nature 310, 271.

Sletvold, N., 2002. Effects of plant size on reproductive output and offspring performance in the facultative biennial *Digitalis purpurea*. Journal of Ecology 90, 958–966.

Spies, T.A., Hibbs, D.E., Ohmann, J.L., Reeves, G.H., Palost, R.J., Swanson, F.J., Whitlock, C., Jones, J.A., Wemple, B.C., Parendes, L.A., Schrader, B.A., 2002. Ecological basis of ecosystem management in the Oregon Coast Range. In: Hobbs, S.D., Hayes, J.P., Johnson, R.L., Reeves, G.H., Spies, T.A., Tappeiner, J.C., Wells, G.E. (Eds.), Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, Oregon, pp. 31–67.

Smith, J.M.B., Harlen, R.L., 1991. Preliminary observations on the seed dynamics of broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. Plant Protection Quarterly 6, 73–78.

Smith, J.W., 2002. Mapping the thermal climate of the H. J. Andrews Experimental Forest, Oregon. MS thesis, Oregon State University.

Snyder, K.U., 2000. Debris flows and flood disturbance in small, mountain watersheds. MS thesis, Oregon State University.

Swanson, F.J., Dyrness, C.T., 1975. Impact of clearcutting and road construction on soil erosion by landslides in the western Cascades or Oregon. Geology 3, 393–396.

Swanson, F.J., James, M.E., 1975. Geology and geomorphology of the H.J. Andrews Experimental Forest, western Cascades, Oregon. Research Paper PNW-188. US Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Swanson, F.J., Johnson, S.L., Gregory, S.V., Acker, S.A., 1998. Flood disturbance in a forested mountain landscape: Interactions of land use and floods. Bioscience 48, 681–689.

Tabacchi, E., Correll, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A. M., Wissmar, R.C., 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40, 497–516.

Tarrega, R., Calvo, L., Trabaud, L., 1992. Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio 102, 139–147.

USDA, NRCS, 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA.

van Baalen, J., 1982. Germination ecology and seed population dynamics of *Digitalis purpurea*. Oecologia 53, 61–67.

van Baalen, J., Prins, E.G.M., 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. Oecologia 58, 84–91.

Vogt, K., Rasran, L., Jensen, K., 2004. Water-borne seed transport and seed deposition during flooding in a small river-valley in Northern Germany. Flora 199, 377–388.

Waloff, N., Richards, O.W., 1977. The effect of insect fauna on growth mortality and natality of broom, *Sarothamnus scoparius*. Journal of Applied Ecology 14, 787–798.

Watterson, N., 2004. Exotic plant invasion from roads to stream networks in steep forested landscapes of western Oregon. MS thesis, Oregon State University.
Wemple, B.C., Jones, J.A., 2003. Runoff production on forest roads in a steep, mountain catchment. Water Resources Research 39, 1220. doi:10.1029/2002WR001744.
Wemple, B.C., Jones, J.A., Grant, G.E., 1996. Channel network extension by logging roads in two basins, western Cascades, Oregon. Water Resources Bulletin 32, 1195–1207.
Wemple, B.C., Swanson, F.J., Jones, J.A., 2001. Forest roads and geomorphic process interactions, Cascade Range, Oregon. Earth Surface Processes and Landforms 26, 191–204.
Williams, P.A., 1981. Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. New Zealand Journal of Botany 19, 31–43.
Wondzell, S.M., Swanson, F.J., 1999. Floods, channel change, and the hyporheic zone. Water Resources Research 35, 555–567.
Wyman, D., 1986. Wyman's Gardening Encyclopedia. Macmillan, New York.