AN ABSTRACT OF THE THESIS OF

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Title: Exotic plant invasion from roads to stream networks in steep forested landscapes of western Oregon.

Abstract approved:

Julia A. Jones

This project explores mechanisms governing the invasion of fluvial systems by two contrasting exotic species in stream networks of steep, relatively remote forested landscapes of western Oregon. This research addresses hypotheses relating limitations of seed source locations, seed transport processes, and sink availability to the distributions of scotch broom (*Cytisus scoparius*) and foxglove (*Digitalis purpurea*) in the H.J. Andrews Experimental Forest (Andrews). *Cytisus scoparius* and *Digitalis purpurea* distributions were mapped along hillslopes and in streams in the Andrews and compared to maps and aerials photographs of flood and geomorphic disturbances. Effects of seed scarification, soaking, and substrate texture on seed germination were investigated using laboratory trials.

Distributions of *Cytisus scoparius* and *Digitalis purpurea* in the Andrews differed greatly and were controlled by interactions between seed sources along roads and invasion sites along streams. The distribution of *Cytisus scoparius* and *Digitalis purpurea* in streams is consistent with limitation by upgradient hillslope seed source locations. The results of this study suggest that *Cytisus scoparius* and *Digitalis purpurea* were present along roads and in clear-cuts in the Andrews from the 1970s to 2003, but invaded the stream network only after geomorphic processes during a large flood in 1996 overcame barriers to stream invasion. Debris flows and flood flows overcame seed dispersal barriers by transporting seeds into the valley bottoms from hillslope source locations along roads and in clear-cut patches. Furthermore, geomorphic processes acting along the stream corridor created suitable conditions for seed deposition, germination, and establishment by removing vegetation and creating sites protected from scour. Seeds were deposited in valley bottoms (sinks) away from scour in middle stream reaches and plants established in these protected locations. This paper outlines a conceptual model highlighting the role of 1996 sinks as seed sources between 1996 and 2003, enabling the invasion to propagate downgradient as a wave into lower reaches of the stream network.

Exotic Plant Invasion from Roads to Stream Networks in Steep Forested Landscapes of Western Oregon

by
Nicholas Watterson

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APPROVED:

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Chair of the Department of Geosciences

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Nicholas Watterson, Author

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INTRODUCTION

Exotic plant invasions are a widespread phenomenon with broad and pervasive effects on the physical and biotic systems of rivers and streams (Vitousek 1990, Mack *et al.* 2000, Tabacchi *et al.* 2000). Recent increased awareness of such impacts and recognition of the rate at which exotic species can invade landscapes has led to large eradication efforts without a firm understanding of how the invasion process operates. Post-invasion eradication measures using pesticides or manual removal are widely used; however, more effective approaches to controlling exotic plant invasion can be developed through improved understanding of the invasion and dispersal process. Plant invasions involve complicated dynamics between the invading species and the environment. Many factors are known to influence exotic plant invasions in a landscape and much work has highlighted the role of roads and streams as corridors for plant dispersal and establishment. Roads may serve as the initial source of seed introduction into a landscape (Parendes 1997, Parendes and Jones 2000). Exotic seeds may be dispersed to roads by intentional planting along roadsides for soil stabilization (Dyrness 1967, 1970, 1975), and seeds may also be introduced by vehicular traffic and spreading of road gravel contaminated with exotic seeds. Once established along roads, invasive plants can disperse more broadly into streams. Despite general recognition of this process, few or no landscape models link interactions between networks such as roads, streams, and debris flows or landslides, to exotic plant dispersal and establishment in the landscape.

In the Pacific Northwest two exotic species are particularly widespread: scotch broom (*Cytisus scoparius* hereafter referred to as *C. scoparius*) and foxglove (*Digitalis purpurea* hereafter referred to as *D. purpurea*). Both *C. scoparius* and *D. purpurea* are capable of expanding their range into stream networks, which is of special concern because of the protected status of many stream environments. Effective control of the invasion of these plants in streams depends on understanding the interplay between roads (seed sources) and hydrologic and geomorphic processes that facilitate exotic plant invasions in stream and river networks through transport and deposition of seeds and preparation of suitable invasion sites (sinks). This paper addresses the mechanisms whereby invasive plant species may be spread from roads into stream networks in steep, forested landscapes of western Oregon. This study focuses specifically on *C. scoparius* and *D. purpurea* in the H.J. Andrews Experimental Forest (hereafter referred to as the Andrews) located in the Cascade Range, Oregon. Although *C. scoparius* and *D. purpurea* are widespread in the Pacific Northwest, they are only in the early stages of invasion along roads and streams in the Andrews Forest, and their spatial patterns have been documented since 1993 (Parendes 1997). In conjunction with other spatial information — long-term records of flood disturbance and maps and aerial images of mass movements and hydro-geomorphic processes — these spatially explicit records of exotic plant distributions along roads provide a unique opportunity to observe the invasion process in a forested landscape. This paper identifies and tests several hypotheses about seed sources, transport and deposition processes, and site factors related to plant invasions from roads to streams in the Andrews forest landscape.

HYPOTHESES

This study investigates the controls on distribution of invasive exotic plants (*C. scoparius* and *D. purpurea*) in stream networks in a steep, forested landscape. Specifically it addresses three hypotheses about how exotic plants are dispersed from roads into stream networks and the hydro-geomorphic dynamics that influence the distribution of exotic species in a stream system.

H_1: Distribution of exotic plants is source-limited. *C. scoparius* and *D. purpurea* seeds are transported mainly by water from populations along roads and in clear-cuts located above streams, into streams.

H_2: Distribution of exotic plants is transport-limited, by water and sediment transport events. *C. scoparius* and *D. purpurea* become established in the streams only after some key transport event, such as a flood or debris flow, transports the seeds into the stream network.

H_3: Exotic plants are limited by the availability of sinks or sites suitable for establishment in the stream network. These are unvegetated sites with fine sediment and which are protected from flood scouring.

BACKGROUND

Plant population behavior can be broken down into four phases: dispersal, recruitment, growth and maintenance, and reproduction (Harper 1977). Here, dispersal is defined as the process by which plant propagules are transported and deposited away from the parent plant. Dispersal is followed by a recruitment phase consisting of seed germination and seedling development at a site. After seedling recruitment the population will grow according to resource availability and environmental conditions, and survivors will eventually grow to reproduce seed and disperse again (Harper 1977). This model of plant population behavior also applies to the process of landscape invasions by exotic plants.

Plants rely on various strategies and mechanisms to disperse propagules, and they have developed biological characteristics to facilitate effective dispersal. Some plants use self-dispersal via gravity or explosive dehiscence to propel seeds away from the parent while others depend on natural processes in the environment such as wind, water, and animals to aid in propagule dispersal (Harper 1977, Willson 1992). Seed morphological adaptations can enable more effective transport by wind, water, and air vectors (Willson 1992). In addition, small seed mass may increase invasive success. Small seeds tend to be produced in greater numbers and may be more easily dispersed and they can have high initial germination rates, shorter dormancy period, or high seedling growth rates, which might facilitate invasion (Rejmanek and Richardson 1996). Human activities such as vehicle traffic, road building, or work and recreational activities can also help disperse seeds over long distances (Howe and Westley 1997, van der Pijl 1982) and even across continents (Salisbury 1961, Elton 1958).

Once propagules are dispersed to a site they must encounter suitable conditions for germination and establishment. Successful seedling recruitment requires compatible environmental conditions. Plant invasions have been linked to physical site conditions such as light levels (Williams 1981, van Baalen 1982, Braithwaite *et al.* 1989, Parendes 1997, Parendes and Jones 2000), soil moisture (Forcella and Harvey 1983, Meekins and McCarthy 2001), substrate texture (Williams 1981) and depth (Williams 1981, Bossard 1993), temperature (Tarrega *et al.* 1992, Bossard 1993) and vegetation structure (Johnstone 1986, Cid-Benevento 1987, Brothers and Springarn 1992). The formation of seed banks, a collection of viable seeds in the soil, and seed dormancy may effectively expand the temporal window for appropriate germination conditions thereby playing an important role in the spread of invasive species (Chambers and MacMahon 1994). After recruited seedlings have emerged and become established [i.e., they are capable of survival independent of seed reserves (Harper 1977)], the plant community continues to be structured by available resources and the environment. Because of environmental conditions, not all seedlings will persist to maturity; however, surviving plants will grow and may eventually mature to produce and disperse seeds. Short juvenile periods and short intervals between seed production may be advantageous characteristics for dealing with changing site resources and environment, and plants with these traits have shown more invasive success (Rejmanek and Richardson 1996).

To successfully invade a landscape, a plant species must overcome all barriers excluding it from a location (Johnstone 1986). These barriers to invasion include 1) biological barriers such as seed production, viability, and dormancy; 2) physical barriers in the landscape like distance, topography, and geomorphology; and 3) environmental barriers such as light and moisture levels, soil conditions, and disturbance frequency (Figure 1) (Parendes 1997, Parendes and Jones 2000). To invade a landscape such as a stream network, a plant species must be able to disperse viable seed from a parent plant (source) to a suitable invasion site (sink) where the seed can germinate and establish.

This research is based upon a conceptual model of how disturbances in a landscape can enable plants to invade stream network sites by overcoming biological, physical, and environmental barriers (Figure 1) (Fox and Fox 1986, Hobbs 1991, Lepart and Debussche 1991). In particular, human disturbances such as traffic and logging activity along road networks may serve to “inoculate” a landscape with propagules of an exotic species

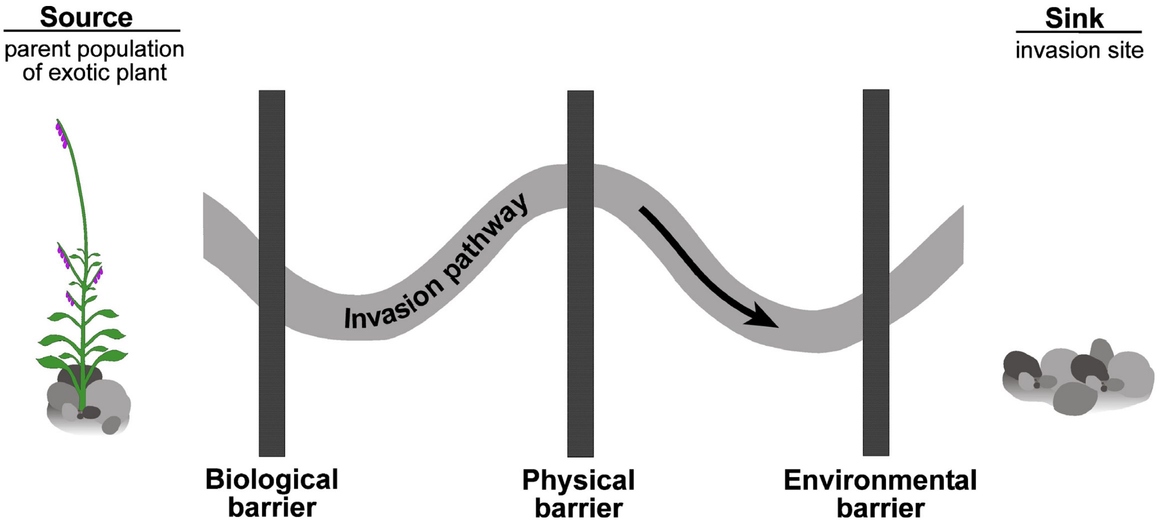

Figure 1. Conceptual model for exotic plant invasions (modified from Parendes and Jones 2000)

(Parendes 1997). Natural processes acting along and between stream and road networks include wind, floods, and — during extreme flood events — mass movements (Wemple *et al.* 2001). These processes can disperse propagules, remove vegetation and deposit fresh sediment, and create light gaps with suitable temperature and moisture levels for plant establishment (Elton 1958, Harper 1977, Westman 1977, Forcella and Harvey 1983, Johnstone 1986, Cid-Benevento 1987, Braithwaite *et al.* 1989, Tyser and Worley 1992, Brothers and Springarn 1992, Johannson *et al.* 1996, Rejmanek and Richardson 1996, Wemple *et al.* 1996, Parendes 1997, Parendes and Jones 2000, Jones *et al.* 2000, Meekins and McCarthy 2001, Wemple *et al.* 2001). Once they are established in the stream network, exotic plant propagules may be mobilized and transported by streamflows and stream geomorphic processes to colonize new sites within the stream network.

Ecology of target species

Cytisus scoparius

C. scoparius is a leguminous perennial shrub in the Fabaceae family, 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, Peterson and Prasad 1998, Leblanc 2001). *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 (Williams 1981, Johnson 1982, Bossard 1991, Rees and Paynter 1997, Paynter *et al.* 1998). Plants typically live for 10 to 12 years in their native environment (Walloff and Richards 1977) although they can survive for as many as 23 years in exotic habitats (Smith and Harlen 1991, Bossard and Rejmanek 1994). *C. scoparius* is tolerant of a wide range of soil conditions but favors dry, sandy soils in full sunlight (Gill and Pogge 1974). Plants are usually 1 to 2 meters (m) tall, but can grow to be 4 m tall (Gill and Pogge 1974, Peterson and Prasad 1998) and can flower and set seed as early as the second year after germination (Peterson and Prasad 1998, Sheppard *et al.* 2002), although most plants flower and set seed in the third or fourth year (Riley 1957, Williams 1981, Paynter *et al.* 1998, Peterson and Prasad 1998, Sheppard *et al.* 2002).

Each mature plant produces tens of thousands of seeds each year (Waloff and Richards 1977, Williams 1981, Bossard and Rejmanek 1994) with high seed viability (Bossard 1993). *C. scoparius* seeds are relatively large, averaging between 2 and 4 (millimeters) mm in length (Gill and Pogge 1974, McAlpine and Drake 2002) with a mean mass of between 5 and 10 milligrams (mg) (Salisbury 1942, Gill and Pogge 1974, Williams 1981, Buckley 2003). Ripe seedpods open explosively, generally dispersing seeds close to the parent plant, often within 1 meter (Bossard 1991, Smith and Harlen 1991, Paynter *et al.* 1996), where they can then be incorporated into the seed bank or transported by other means. Because of the relatively large size and weight of *C. scoparius* seeds, they are not likely to be dispersed long distances by air (e.g., Bossard 1991, Smith and Harlen 1991, Paynter *et al.* 1996) and without the assistance of more powerful external forces like water. Ants can disperse these seeds locally (<5m), but animals like mice, grouse, quail, and deer, that are capable of transporting some kinds of seeds greater distances, are not effective dispersers of *C. scoparius* seed (Bossard 1991). Seeds are hard-coated and can remain viable in the seed bank for many years to decades (Turner 1933 as cited in Gill and Pogge 1974, Smith and Harlen 1991, Bossard 1993). Common nursery practice involves propagation from cuttings (Wyman 1986); however, *C. scoparius* vegetative regeneration from transported plant parts has not been observed in nature (Peterson and Prasad 1998, USDA 2004).

Digitalis purpurea

D. purpurea is a semalparous (single-reproducing) to iteroparous (multiple-reproducing) facultative biennial or short-lived perennial in the Scrophulariaceae family, native to Europe (van Baalen and Prins 1983, 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 (Salisbury 1942, Harper 1977, van Baalen 1982, Sletvold 2002), and it particularly favors high light, high temperatures, and moderate soil moisture levels (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). Although highly variable, an individual plant produces on average between 33,000 and 86,000 and as many as 500,000 seeds (Salisbury 1942, Sletvold 2002). *D. purpurea* is typically monocarpic, dying after fruit production; 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 (Ashley *et al.* unpublished document) and weighing from 0.08 to 0.09 mg (Salisbury 1942, van Baalen 1982, Sletvold 2002). Seeds are passively dispersed from the parent, likely an average distance of 4 m (Hanson 2000), where they can remain viable in the seed bank for years (van Baalen 1982) or transported by wind or other processes. *D. purpurea* is not known to reproduce vegetatively from transported plant parts (USDA 2004).

Study area

The Andrews is equal to the Lookout Creek catchment, and it encompasses 6400 hectares (ha) or 64 square kilometers (km^2) located approximately 80 km east of Eugene in the western Cascade Range of Oregon (Figure 2). The Andrews is characterized by deeply dissected topography of forested ridges and valleys. Elevations range from 415 to 1615 m. Below elevations of 1000 m the geology consists of late Oligocene to early Miocene hydrothermally altered and geomorphically unstable volcaniclastic rocks. Above 1000 m bedrock and soil are derived from middle to late Miocene andesitic and basaltic lava flows (Swanson and James 1975). The Andrews has a mild maritime climate with dry summers and wet winters. Mean monthly temperatures vary with elevation, but maximum monthly temperatures range from between 19 degrees Celsius (C) and 28 C in July and August to between 2 C and 5 C in December and January; monthly minimum temperatures are typically between 8 C and 10 C in July and August and range from –2 C to 1 C during December through March (Figure 3) (Smith 2002). Low-elevation annual precipitation averages 230 centimeters (cm), falling mostly as rain between November and March. Average annual precipitation at higher elevations is more than 355 cm with snowfall more common. Native coniferous forest of Douglas fir (Pseudotsuga menziesii) and Western Hemlock (Tsuga heterophylla) from 80 to more than 500 years old, covers most of the landscape (H. J. Andrews 2004).

Lookout Creek is a fifth-order stream at its base with over 138 km of stream network draining the 6400-hectare Andrews Forest (Wemple *et al.* 1996). Stream environments range from high-gradient bedrock channels to wide alluvial stretches formed upstream of valley floor constrictions (Grant and Swanson 1995). Much of the network consists of boulder-dominated, stepped-bed channel reaches with alternating pools and steep units (Grant *et al.* 1990). Lookout

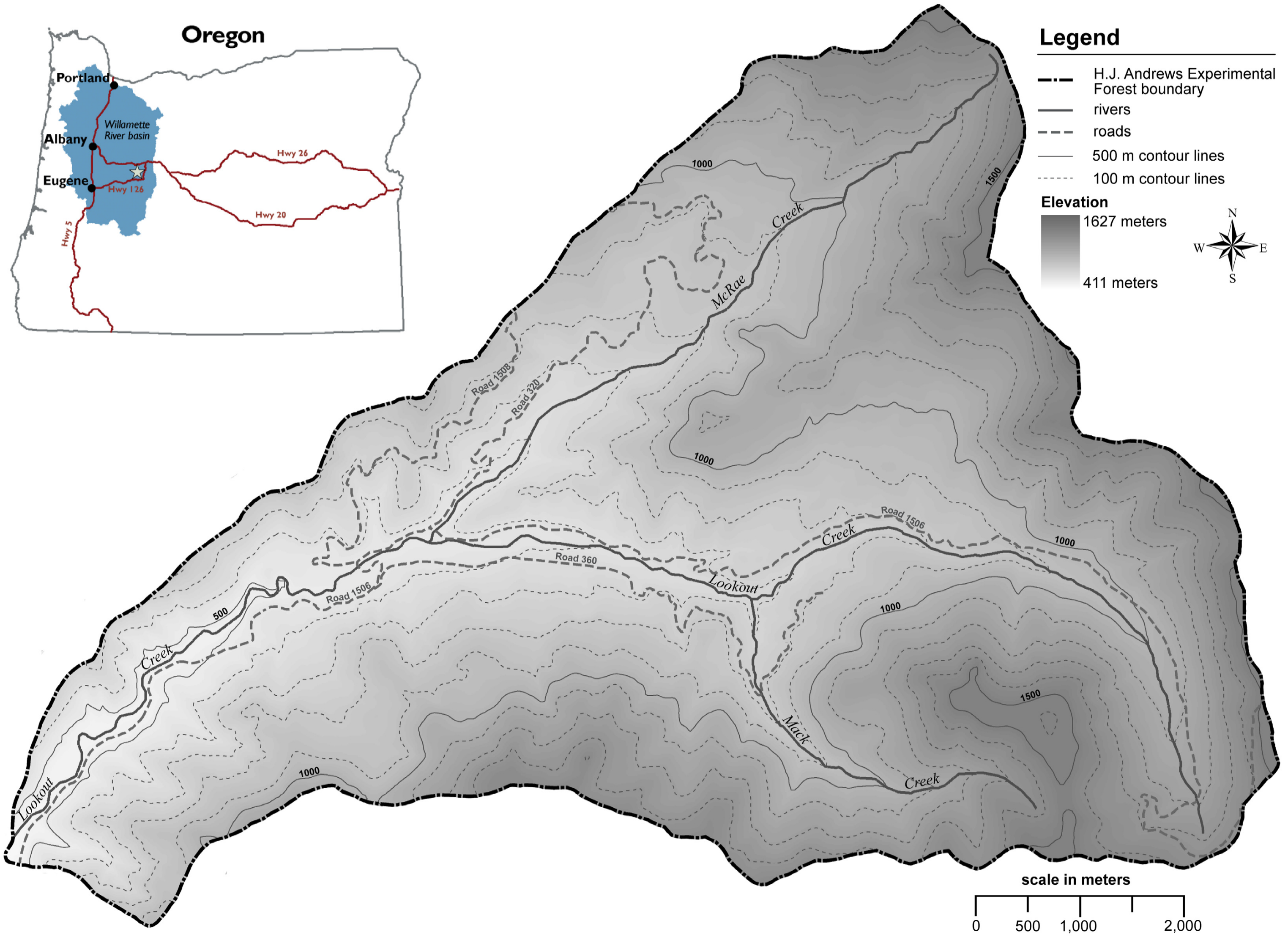

Figure 2. Study site location map

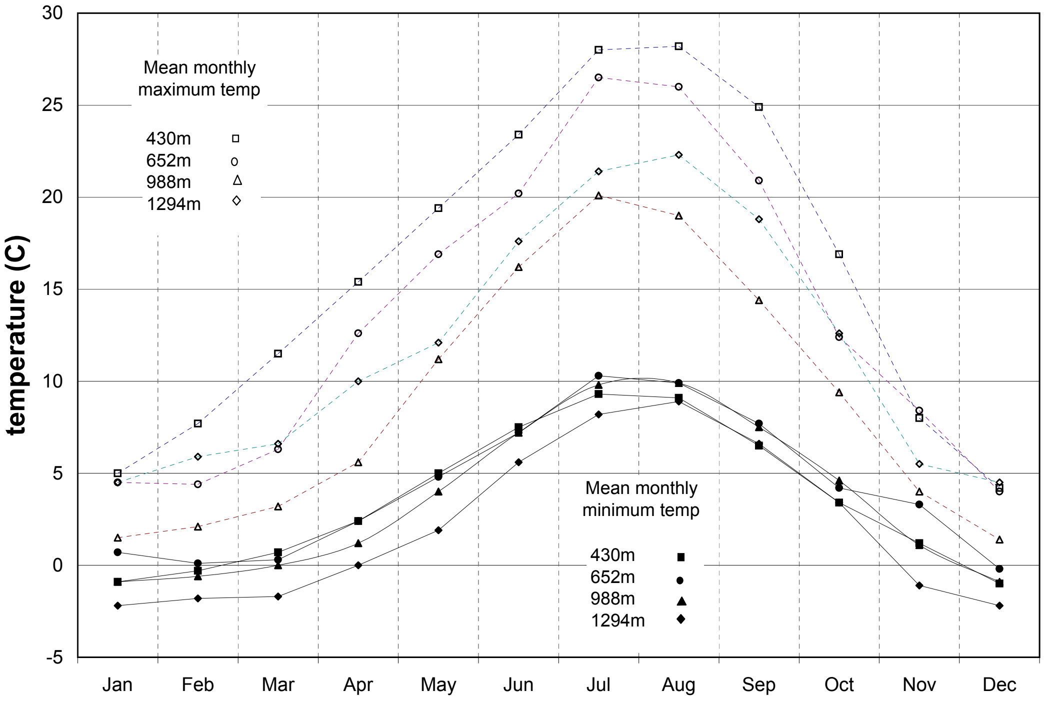

Figure 3. Mean monthly temperature by elevation in the Andrews (Smith 2002)

Creek has two major tributaries, Mack Creek (third-order) and McRae Creek (fourth-order). Historic disturbances, including large floods in 1964 and 1996, have strongly configured the landscape (Swanson *et al.* 1998, Wondzell and Swanson 1999). Debris flows and slides have shaped steep headwater stream channels and hillslopes; extreme floods rework broad unconstrained alluvial valley floors and remove or severely damage riparian vegetation (Swanson *et al.* 1998).

The road network in the Andrews 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 Andrews entrance (Wemple *et al.* 1996). Roads were constructed to access dispersed patch clear-cuts, which cumulatively affected 25% of the Andrews over the period from 1949 to 1990 (Jones and Grant 1996). Roads can function both as initiation and deposition sites for geomorphic processes, but their net effect is to increase sediment production especially in midslope positions (Wemple *et al.* 2001). In addition, hydrologic linkages between the road and stream network at hundreds of road-stream crossings can extend the stream network (Wemple *et al.* 1996, Wemple and Jones 2003) and may increase peak flows by routing runoff along roads into streams (Jones and Grant 1996).

1996 flood

In February 1996 Lookout Creek experienced a flood with an instantaneous peak discharge that was nearly four times the average annual peak discharge for the 50 year period prior (1950 to 2001) and the largest peak in Lookout Creek since flow gauging started in 1950 (Figure 4). This flooding triggered widespread landscape change (Swanson *et al.* 1998). During this event runoff processes along road networks (Wemple and Jones 2003) and debris flows along tributary channels (Wemple *et al.* 2001) transported water and sediment from roads into mainstem streams. In 1996 debris flows scoured long stretches of the stream network (Snyder 2000) and high-energy floodwaters reworked and altered channel sediment and structures in mainstem reaches of Lookout Creek and McRae Creek (Wondzell and Swanson 1999) and removed riparian vegetation (Johnson *et al.* 2000). The 1996 flooding was closely followed by floods in 1997, 1999, and 2000 with peak discharges of 1.5 to 1.7 times the average annual peak discharge. Between 1996 and 2000, Lookout Creek experienced four of the eight largest annual peak flows in the last 53 years (Figure 4).

Previous studies of exotic species at the Andrews

Dates of introduction of *C. scoparius* and *D. purpurea* in the Andrews are unknown. According to *Franklin and Dyrness* (1971), the forest was relatively undisturbed until logging and road building began in 1950 except for sheep grazing and burning along ridges in the late 1800s to early 1900s (S. Takaoka, personal communication) and wildfires (Weisberg 1998). It is probable that most exotic species were not present, or present only in small numbers, until road construction and logging began in the late 1940s (Parendes and Jones 2000). By 1971, both

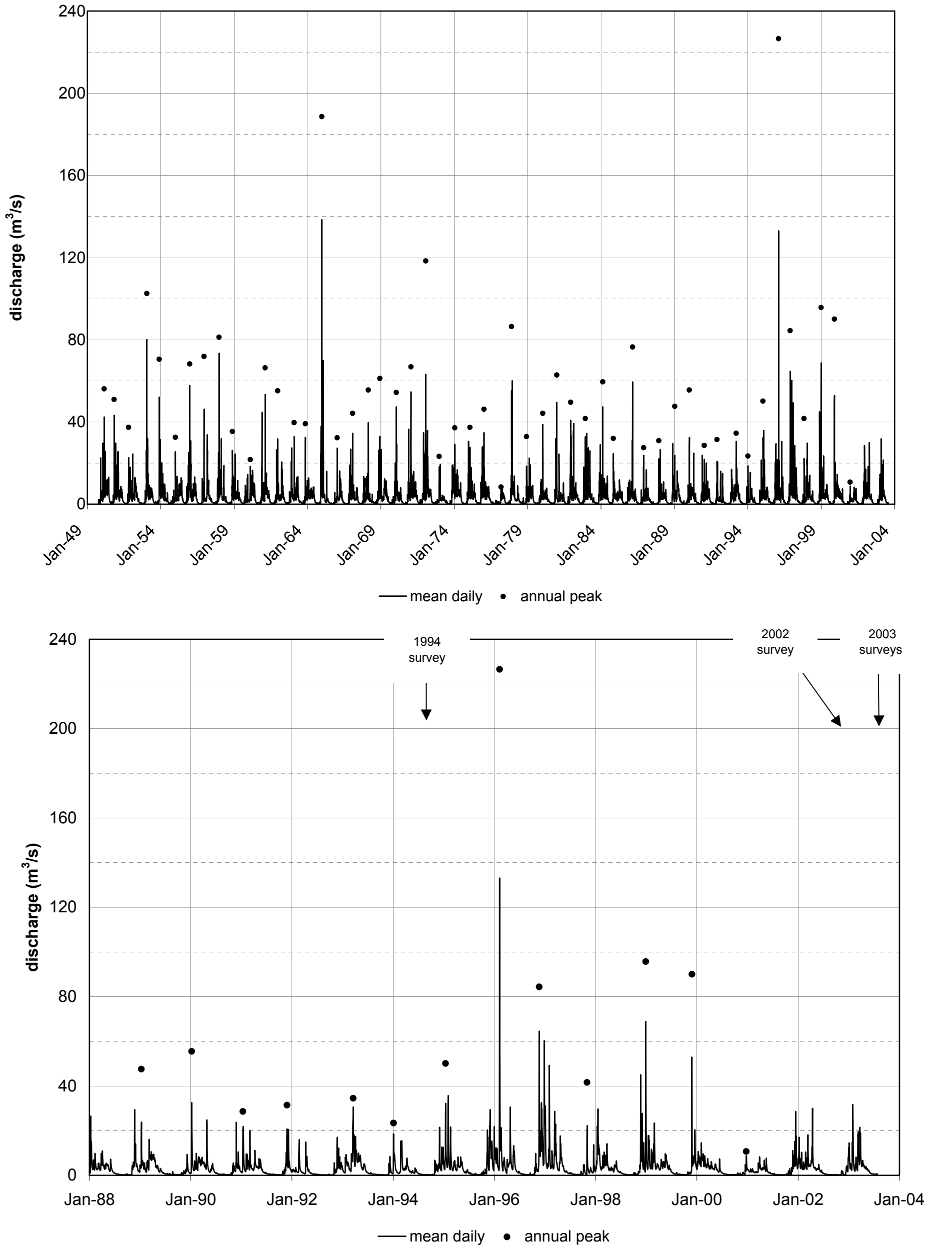

Figure 4. Historical discharge at lower Lookout Creek gauging station (USGS/USFS)

D. purpurea and *C. scoparius* were present in the Andrews (Franklin and Dyrness 1971) with *C. scoparius* occurring along sections of road, in harvest patches, and at a quarry along Road 1506 (Franklin and Dyrness 1971; J. Franklin, personal communication). *D. purpurea* was first present only in harvest patches (Franklin and Dyrness 1971).

In 1994 *Parendes* (1997) documented the distributions of *C. scoparius* and *D. purpurea* along roads while surveying the presence of eight invasive plant species in the Andrews road network (Parendes 1997, Parendes and Jones 2000). Parendes (1997) drove 105.8 km of the Andrews road network (89% of the current road network), and mapped the presence of exotic plant species within a 2-m road buffer along 0.1-mile (0.16 -km) road segments (Parendes unpublished data, Parendes 1997, Parendes and Jones 2000). In 1994 *C. scoparius* was observed along 11.8 km (11.2%) of the road network and *D. purpurea* was observed along 0.8 km (0.8%) of roads (Figure 5) (Parendes unpublished data). *C. scoparius* and *D. purpurea* were among the least common of the 8 exotic species investigated (Parendes 1997). Parendes (1997) also surveyed 2.5 km of streams in the Andrews but observed no *C. scoparius* or *D. purpurea*. The road survey was replicated again in 2002 at which time *C. scoparius* and *D. purpurea* were present along 13.5 km (12.8%) and 4.5 km (4.3%) of the road network surveyed, respectively (Figure 5) (Cilenti unpublished data). Additionally, in September 2002 a small study was conducted to investigate exotic plants in other parts of the landscape (Ashley *et al.* unpublished document). This research involved surveying approximately 3 km of stream network, 18 km of roads, three debris flow paths, and timber harvest patches. This study was the first to document the presence of both *D. purpurea* and *C. scoparius* in the Andrews streams and represented an early attempt to reconstruct the dispersal of exotic plants beyond the road network. It also demonstrated the need for further research to examine interacting effects of road and stream networks and timber harvest patches on the dispersal and distribution of exotic plants across a landscape.

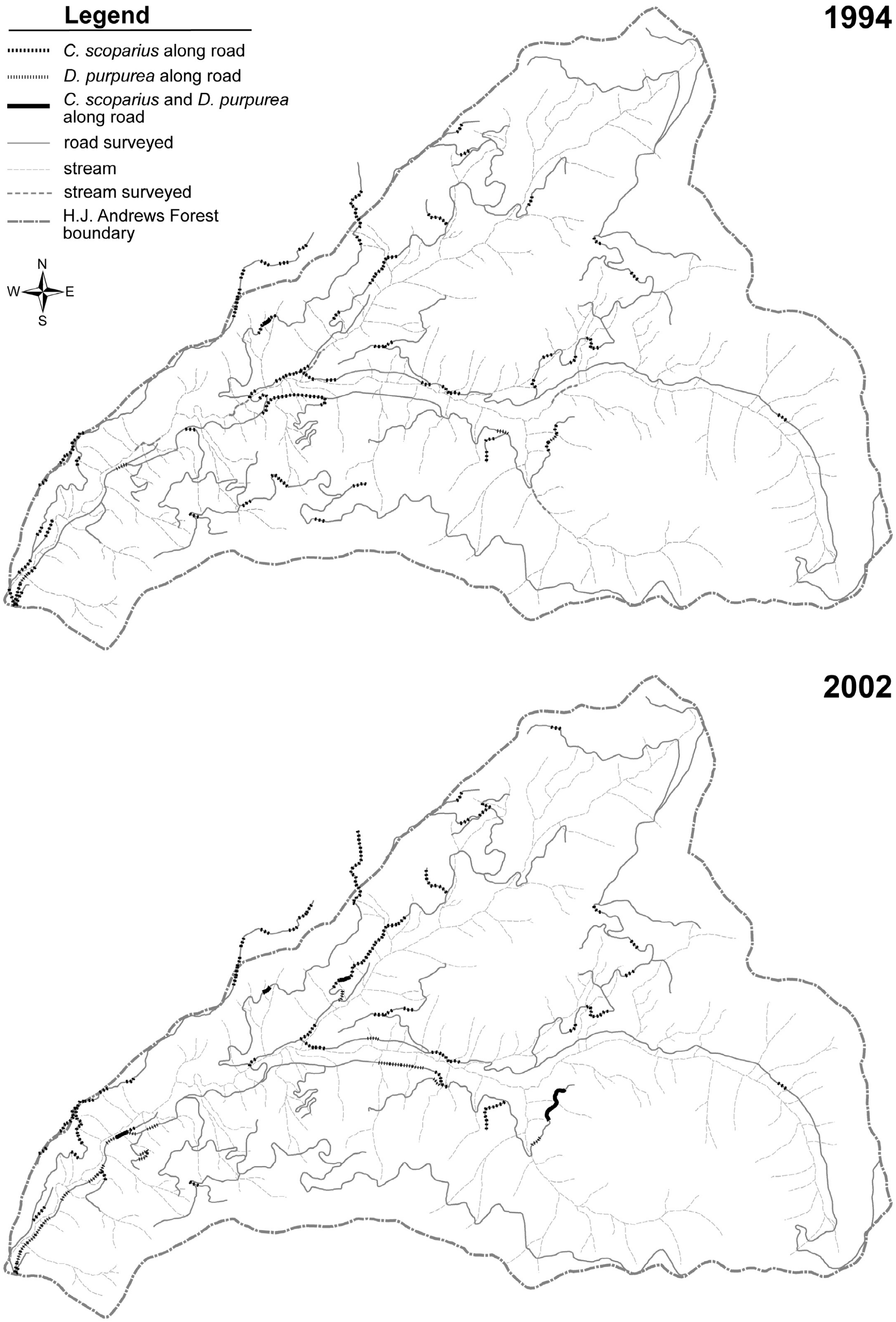

Figure 5. Map of *Cytisus scoparius* and *Digitalis purpurea* occurrences along the Andrews road network in 1994 and 2002. Figure shows the results from previous road and stream surveys conducted in 1994 (Parendes unpublished data) and a road survey in 2002 (Cilenti unpublished data).

METHODS

This study involved three analyses: 1) mapping the spatial pattern of the two target species in the landscape with field surveys, 2) conducting germination trials to understand how seed transport or dispersal processes may affect the viability and subsequent germination success of seeds, and 3) using GIS and spatial analysis to examine links between processes and patterns in the invasion of *C. scoparius* and *D. purpurea* across the landscape.

Field surveying

Between July 1 and July 14, 2003, all third-order and higher streams (a total of approximately 24 km of streams) in the Andrews were surveyed for the presence of *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 exotic plant densities (Parendes and Jones 2000). At each location where a *C. scoparius* or *D. purpurea* plant or population was present, where possible a global positioning system device (GPS) was used to obtain an accurate location. Plant characteristics including species, population, size, and health were noted and environmental conditions such as light level and substrate texture and moisture were recorded. Each site was sketched and lateral and vertical measurements were made from plant locations to prominent structures such as the active channel, the riparian forest, side or high-water channels, head of channel bar, terrace or floodplain edge, or other notable features like large wood and logs. Additional field descriptions of the depositional environment and likely modes and mechanisms of dispersal were made. Sites were digitally photographed for further documentation and reference.

Also during July 2003, 48.1 km of roads in the vicinity of, or directly crossing, third-order or higher streams were surveyed to record the locations of *C. scoparius* and *D. purpurea* along the road network. This road survey was designed to supplement a comprehensive survey of the road network conducted the year prior in 2002 by *Cilenti* (unpublished data). Road segments with plants along or adjacent to the road were recorded and located by GPS when possible. Approximate population counts, substrate texture, light levels, and other site characteristics were documented and potential mechanisms for dispersal to the area were described.

GIS analysis

Spatial analysis of the distribution patterns of *C. scoparius* and *D. purpurea* was conducted using a GIS of the Andrews created in ArcGIS (ESRI, Redlands,CA) with a 10-m digital elevation model (DEM) to represent topography and overlain with spatial layers of the Forest boundary, road network, hydrography, and historic harvesting activities (H. J. Andrews 2004). For finer spatial analysis of the stream network and to investigate changes in stream geomorphology over time and particularly in response to the 1996 flood event, United States Forest Service (USFS) color aerial photos from September 1990 and September 1996 were scanned, georeferenced, and overlain in the GIS for selected reaches of Lookout Creek. In addition, United States Geological Survey (USGS) digital orthophoto quadrangles (DOQs) from September 2000 were included to improve temporal resolution for analyses of changes in stream geomorphology. Using GPS coordinates, field sketches and photographs, and aerial photos and DOQs, data collected during the 2003 field survey of the Andrews streams were plotted as point features. Detailed polygons showing the areal extent of *C. scoparius* and *D. purpurea* occurrence sites were also digitized with attribute data on plant species, population, distance from active channel, and elevation above active channel. These data were ultimately included in a database of the USFS Data Bank (www.fsl.orst.edu/lter). Occurrences of *C. scoparius* and *D. purpurea* along roads were displayed by attributing a dynamically segmented road layer (0.1-mile road segments) used in previous studies at the Andrews by *Parendes* (1997, unpublished data) and *Cilenti* (unpublished data) with *C. scoparius* and *D. purpurea* presence or absence. Lastly, spatial data showing debris flow paths occurring between 1946 and 1996 (Snyder unpublished data) were included in the GIS.

After compiling all data in the GIS, exotic plant occurrences in the streams were divided into discrete patches using field notes and information in the GIS. Sites where one or more *C. scoparius* or *D. purpurea* plants were found were called patches. For GIS analysis, the minimum grain size of patches was considered to be 10 m for *C. scoparius* and *D. purpurea*. When sites consisted of larger populations spread over longer lengths of the stream, the patch size was defined as the distance between the upper- and lower-most plants at a site. *C. scoparius* plants located more than 10 m from other *C. scoparius* individuals were assigned to separate patches. In the case of *D. purpurea*, plants within 25 m of other individuals were counted as part of a single patch. *D. purpurea* plants with separations of more than 25 m were assigned to different patches. Additionally, for both *C. scoparius* and *D. purpurea*, plants located on the opposite side of the low flow stream channel were assigned to different patches (Table 1). The distances used to define patches and patch spacing was chosen to group individual plants that could have been created from dispersal without water; interpatch distances were chosen to separate patches which were likely to have been created through seed dispersal by water.

Table 1. Criteria for defining *Cytisus scoparius* and *Digitalis purpurea* patches in streams

	Cytisus scoparius	*Digitalis purpurea*
within patch distance	<10 m	<25 m
between patch distance	≥ 10 m	≥ 25 m
	or opposite side of channel	

C. scoparius has a relatively large and heavy seed (Salisbury 1942, Gill and Pogge 1974, Williams 1981, McAlpine and Drake 2002) and is commonly dispersed only short distances from the parent (Bossard 1991, Smith and Harlen 1991, Paynter *et al.* 1996) suggesting that longer dispersal, particularly over water, may be facilitated only by external physical processes (e.g., water transport). *D. purpurea* seed are small and light (Salisbury 1942, van Baalen 1982, Sletvold 2002, Ashley *et al.* unpublished document) and as a result may be subject to local transport by wind. Dispersal distances for *D. purpurea* by passive autochory (self dispersal) are believed to be approximately 4 m (Hanson 2000), but can exceed 5.5 m with wind velocities of 3.9 meters per second (m/s) and 7.5 m/s at dispersal heights of 1.5 m and 1 m, respectively (Bruelheide and Heinemeyer 2002). Studies of wind dispersal on surfaces with varying textures suggest that wind-related seed dispersal distances decrease and elapsed time to seed movement increase with increasing coarseness of the surface, especially when seed size and mass are small (Chambers *et al.* 1991, Johnson and Fryer 1992). *D. purpurea* seeds are small and mean bed particle sizes are generally large in the Andrews stream network [between 10 and 15 cm (Swanson 2002)]. Nevertheless, because of the potential for local seed dispersal by wind, a larger distance of 25 m was used to define separate *D. purpurea* patches. As with *C. scoparius*, *D. purpurea* seed dispersal across the active stream channel is likely to require transport by water.

Experimental trials

Experimental trials were designed to address two principal questions: 1) whether *C. scoparius* and *D. purpurea* seeds are capable of surviving transport by geomorphic processes (e.g., entrainment in debris flows, as stream bedload, in flowing water, and 2) whether there is a relationship between substrate texture and *C. scoparius* and *D. purpurea* seed germination which might account for the distribution of plants in the stream network. Germination trials were conducted between August and October 2003 using commercially acquired *C. scoparius* (Carter Seeds, Vista, California) and *D. purpurea* (Ed Hume Seeds, Inc., Puyallup, Washington) seeds. Seeds were subjected to treatments of mechanical scarification by tumbling with sediment and water; other seed samples were germinated in different substrates to evaluate whether substrate texture effects the germination rate of seeds. Sediment and water for the experiments were collected from Lookout Creek. To sterilize the sediment and kill any seeds that might be present, all sediment was baked at 121 C for 2.5 hours. The oven-dried sediment was dry-sieved and divided into 12 grain-size categories — very coarse gravel, coarse gravel, medium gravel, fine gravel, very fine gravel, very coarse sand, coarse sand, medium sand, fine sand, very fine sand, silt, and clay [following American Society of Civil Engineers (ASCE) classification] — for use in the germination trials.

Scarification trials

To evaluate potential effects of transport of seeds by debris flows and fluvial processes on seed viability, 18 scarification (tumbling) treatments were administered to *C. scoparius* and *D. purpurea* seed samples. For each treatment, 100 *D. purpurea* and 60 *C. scoparius* seeds were used. *D. purpurea* seed samples were selected at random from a larger population of seeds; *C. scoparius* seeds were first sorted visually to separate seeds with obvious physical deformities (e.g., they were hollow, crushed, or had other surface defects) from the rest of the seed lot, and then samples were randomly chosen from this resulting population of seeds. Each seed sample was placed with a sediment and streamwater mixture in a manually-cranked tumbler constructed from a cylindrical one-gallon paint canister (inside diameter of 16.2 cm, length of 18.9 cm, circumference of 50.9 cm or 0.51 m) lined with rubber and with attached rotating handle (Figure 6).

Figure 6. Tumbler used in scarification trials

The mixture of sediment and water and tumbling amounts varied in each of the 18 scarification treatments (Tables 2 and 3). Seeds were tumbled between 100 and 2000 times in different sediment and water mixtures. At the conclusion of the tumbling, seeds were retrieved from the tumbler for planting. *C. scoparius* seeds were removed from the sediment and water mixture by hand with tweezers; *D. purpurea* seeds are very small and required a more complicated retrieval method. All sediment and water in the tumbler was first rinsed through an approximately 1-mm sieve and then through a smaller mesh of 297 microns (μm).

Table 2. *Cytisus scoparius* scarification treatments

Sample number	Treatment type	Sample size	Tumbling details			Scarification mixture composition			
			# rotations	*duration (min)*	*mixture type*	*sediment (%)*	*water (%)*	*sediment (ml)*	*water (ml)*
1	control	50	---	---	---	---	---	---	---
2	control	50	---	---	---	---	---	---	---
3	optimal	50	---	---	---	---	---	---	---
4	floats	50	---	---	---	---	---	---	---
5	sinks	50	---	---	---	---	---	---	---
6	tumbled	50	100	2	very coarse sand	50	50	200	200
7	tumbled	50	500	10	very coarse sand	50	50	200	200
8	tumbled	50	1000	20	very coarse sand	50	50	200	200
9	tumbled	50	2000	40	very coarse sand	50	50	200	200
10	tumbled	50	100	2	fine gravel	50	50	200	200
11	tumbled	50	500	10	fine gravel	50	50	200	200
12	tumbled	50	1000	20	fine gravel	50	50	200	200
13	tumbled	50	2000	40	fine gravel	50	50	200	200
14	tumbled	50	100	2	v.c. sand/f. gravel mix	100	0	200	0
15	tumbled	50	100	2	v.c. sand/f. gravel mix	75	25	200	67
16	tumbled	50	100	2	v.c. sand/f. gravel mix	50	50	200	200
17	tumbled	50	100	2	v.c. sand/f. gravel mix	25	75	67	200
18	tumbled	50	100	2	v.c. sand/f. gravel mix	0	100	0	200
19	tumbled	50	1000	20	v.c. sand/f. gravel mix	100	0	200	0
20	tumbled	50	1000	20	v.c. sand/f. gravel mix	75	25	200	67
21	tumbled	50	1000	20	v.c. sand/f. gravel mix	50	50	200	200
22	tumbled	50	1000	20	v.c. sand/f. gravel mix	25	75	67	200
23	tumbled	50	1000	20	v.c. sand/f. gravel mix	0	100	0	200

Sediment type classification based on American Society of Civil Engineers (ASCE) and National Research Council standards.
very coarse sand = 1 to 2 mm diameter, fine gravel = 4 to 8 mm diameter

Table 3. *Digitalis purpurea* scarification treatments

Sample number	Treatment type	Sample size	Tumbling details			Scarification mixture composition			
			# rotations	*duration (min)*	*mixture type**	*sediment (%)*	*water (%)*	*sediment (ml)*	*water (ml)*
1	control	100	---	---	---	---	---	---	---
2	control	100	---	---	---	---	---	---	---
3	correction	100	1	---	very coarse sand	50	50	200	200
4	correction	100	1	---	very coarse sand	50	50	200	200
5	correction	100	1	---	fine gravel	50	50	200	200
6	correction	100	1	---	fine gravel	50	50	200	200
7	tumbled	100	100	2	very coarse sand	50	50	200	200
8	tumbled	100	500	10	very coarse sand	50	50	200	200
9	tumbled	100	1000	20	very coarse sand	50	50	200	200
10	tumbled	100	2000	40	very coarse sand	50	50	200	200
11	tumbled	100	100	2	fine gravel	50	50	200	200
12	tumbled	100	500	10	fine gravel	50	50	200	200
13	tumbled	100	1000	20	fine gravel	50	50	200	200
14	tumbled	100	2000	40	fine gravel	50	50	200	200
15	tumbled	100	100	2	v.c. sand/f. gravel mix	100	0	200	0
16	tumbled	100	100	2	v.c. sand/f. gravel mix	75	25	200	67
17	tumbled	100	100	2	v.c. sand/f. gravel mix	50	50	200	200
18	tumbled	100	100	2	v.c. sand/f. gravel mix	25	75	67	200
19	tumbled	100	100	2	v.c. sand/f. gravel mix	0	100	0	200
20	tumbled	100	1000	20	v.c. sand/f. gravel mix	100	0	200	0
21	tumbled	100	1000	20	v.c. sand/f. gravel mix	75	25	200	67
22	tumbled	100	1000	20	v.c. sand/f. gravel mix	50	50	200	200
23	tumbled	100	1000	20	v.c. sand/f. gravel mix	25	75	67	200
24	tumbled	100	1000	20	v.c. sand/f. gravel mix	0	100	0	200

*Sediment type classification based on American Society of Civil Engineers (ASCE) and National Research Council standards.
very coarse sand = 1 to 2 mm diameter, fine gravel = 4 to 8 mm diameter

Previous tests had shown that all *D. purpurea* seeds passed the 1-mm screen but were retained by the 297-µm screen. To ensure that all seeds were given a chance to germinate, including those that may have been pulverized during the tumbling treatment, all material collected on the 297-µm screen (both seeds and sediment) was planted for germination.

All seeds were germinated on moist blotter paper under controlled conditions of 20 C with 8 hours light and 16 hours dark at the Oregon State University Seed Laboratory. Fifty of the 60 *C. scoparius* seeds that had been treated were placed on a 13-cm by 24-cm blotter paper moistened with stream water, enclosed in a clear plastic box to prevent desiccation, and placed in the germinator on August 26, 2003. *D. purpurea* samples were retrieved from the tumbler and sieved and then spread evenly on the moistened blotter and germinated in the same manner. Seeds were examined every few days during the first month after planting and germinated seeds (radicle emerging at least 1 mm) were counted and removed. Blotter papers were moistened when necessary and any moldy seeds were also removed at these times. The interval between examinations increased until seeds were being examined once every two weeks after 164 days and at termination of the *C. scoparius* trials on February 6, 2004. The *D. purpurea* trials were terminated earlier after 50 days on October 15, 2003.

Control samples were also germinated for both species. For *C. scoparius*, these controls included two replicate samples of untreated seeds, one “optimally” treated sample of seeds soaked for 2 hours in 55 C streamwater (Carter Seeds, Vista, California), 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 sets of two samples of *D. purpurea* seed recovery correction trials. Two replicate correction trials were conducted to evaluate the baseline seed recovery after tumbling with very coarse sand; two replicate trials were also conducted to determine the percent seed recovery after tumbling with fine gravel. In each of these correction trials, 100 *D. purpurea* seeds were added to sediment and water in the tumbler, rotated once to mix the sediment and seed (but not to cause any seed mortality), and then retrieved from the tumbler through the same screening process as was used for the *D. purpurea* tumbling treatments. As with the tumbling treatments, all material retained on the 297-μm screen was planted and germinated. Based on the germination rate of the correction trials and assuming that the germination rate of the two untreated samples represented the maximum germination under the planting conditions in this study, germination rates in the tumbling trials were adjusted to account for seed losses that occured during the seed recovery process of the tumbling treatments.

Substrate trials

A second set of germination trials was conducting in substrates of seven different compositions to determine whether plant distribution patterns in the field might be a result of germination and establishment in different substrates as opposed to a reflection of dispersal processes alone. For both *C. scoparius* and *D. purpurea*, 350 randomly selected seeds — from the same seed lots used in the tumbling trials — were administered "optimal" treatments (warm water soak described earlier for *C. scoparius* and no treatment for *D. purpurea*) (Table 4). For each of the species and each of seven sediment textures (i.e., coarse gravel, medium gravel, very fine gravel, coarse sand, medium sand, a mixture of fines, and a mixture of very coarse gravel and medium sand) two replicate samples of 25 "optimally" treated seeds were planted in square

Table 4. *Cytisus scoparius* and *Digitalis purpurea* substrate treatments

Pre-treatment	Sample size	Number of replicates	Substrate type	Substrate mixture		Sediment particle size range	
				*particle type**	*% by volume*	*(μm)*	*(mm)*
Optimal	25	2	sand and gravel mix	very coarse sand	70	32,000-64,000	32-64
				medium gravel	30	250-500	0.25-0.5
Optimal	25	2	coarse gravel	coarse gravel	100	16,000-32,000	16-32
Optimal	25	2	medium gravel	medium gravel	100	8,000-16,000	8-16
Optimal	25	2	very fine gravel	very fine gravel	100	2,000-4,000	2-4
Optimal	25	2	coarse sand	coarse sand	100	500-1,000	0.5-1
Optimal	25	2	medium sand	medium sand	100	250-500	0.25-0.5
Optimal	25	2	fines	fine sand	33	125-250	0.125-0.25
				very fine sand	33	64-125	0.064-0.125
				silt and clay	33	<64	<0.064

*Sediment type classification based on American Society of Civil Engineers (ASCE) and National Research Council standards.

plastic pots, 9.5 centimeters (cm) wide by 8.5 cm deep for *C. scoparius* and 8.5 cm wide by 8 cm deep for *D. purpurea*, filled three quarters full with sediment. Seeds were planted in an evenly-spaced design in the pots and covered with approximately 1 cm of sediment. In the mixture of very coarse gravel and medium sand, pots were filled approximately three quarters full with gravel, sand was poured over the gravel, seeds were planted, and additional sand was poured over the seeds. Even spacing between seeds was more difficult to achieve in this very coarse sand and gravel mixture because of the large size of the very coarse gravel particles. In this case seeds were dropped from above the sediment at even spacing and were allowed to rest where they landed, oftentimes unevenly spaced in the sediment. Furthermore, the large particle sizes made it difficult to ensure a consistent 1-cm planting depth. Table 4 summarizes and gives additional details of the treatments in the substrate germination trials.

Once planted, the pots were saturated with stream water, allowed to drain, covered with plastic wrap, and placed in indirect natural light at room temperature conditions fluctuating between approximately 15 C and 24 C. After planting on August 24, 2003 the pots were examined every few days during the early trial period. During each examination, germinated seeds were counted and removed, and when necessary the sediment was remoistened. Seeds were considered germinated when a seedling emerged through the substrate surface. By the end of the *C. scoparius* trial on January 29, 2004 after 158 days, the interval between examinations of the pots was approximately two weeks. The *D. purpurea* substrate trials were terminated earlier on September 27, 2003 after an approximately two-week interval in which no seeds emerged.

Viability testing and flotation trials

Tetrazolium chloride tests were run on separate samples of untreated *C. scoparius* and *D. purpurea* seeds to detect the presence of living tissue and determine the viability of the *C. scoparius* and *D. purpurea* seeds used in the germination trials. Two replicates of *C. scoparius* seeds (n = 95 each) and two replicates of *D. purpurea* seeds (n = 102 and 97) were tested for viability using the tetrazolium chloride method. All tetrazolium chloride viability testing was performed at the Oregon State University Seed Laboratory.

Flotation trials in water were also conducted to understand the floating abilities of both species of seed. Ten replicates of *C. scoparius* seeds (n=25) and ten replicates of *D. purpurea* seeds (n=25) were separately placed in 20 glass containers filled with 150 ml of Corvallis tap water. The containers were vigorously disturbed at intervals of 12 hours to break the water surface tension and any adhered seeds before recording the floating status of the seeds. The number of germinated *D. purpurea* seeds was also noted during the course of the trials. Flotation trials were conducted between January 23 and February 7, 2004.

RESULTS

Plant distributions at the catchment scale

C. scoparius occurred along 5.7 km (11.9%) of roads surveyed in 2003, but occupied only 100 m (0.4 %) of 24 km of surveyed streams in 2003 (Figure 7). Only approximately 25 plants were observed at ten different sites on fluvial landforms in the middle reaches of McRae and Lookout creeks in 2003 (Figure 8). As of summer 2003, *C. scoparius* was still relatively uncommon in the stream system despite having occurred along a total of 19 km (18%) of the road network surveyed during the previous decade (1994, 2002, or 2003 road surveys) at elevations of 400 m up to 1100 m (Figure 9). All but one of the *C. scoparius* patches observed in the stream network in 2003 were located in the general vicinity and downgradient of high-use road intersections (bridge crossings or adjacent roads) where *C. scoparius* had been present since 1994 (Figures 9 and 10). Although *C. scoparius* was present along roads higher up in the catchment, interactions between mainstem stream channels and roads occupied by *C. scoparius* were infrequent or nonexistent at these high elevations.

D. purpurea occurred along 3.2 km (6.7%) of the 48.1 km of roads surveyed during the summer of 2003 and was observed at 49 sites in the stream network. In 2003, *D. purpurea* patches occupied approximately 1.3 km (5.4%) of the surveyed stream length (Figure 7) and had a total estimated population of approximately 539 individual plants. From 1994 to 2003 *D. purpurea* occurred along a total of 6.1 km (5.8%) of the roads surveyed (Figures 11 and 12). In 2003, *D. purpurea* occured on hillslopes in the Lookout Creek catchment below an elevation of approximately 800 m and in the stream below 700 m; in McRae Creek, *D. purpurea* occurred only below 740 m on hillslopes and below 600 m in the stream. The spatial extent (i.e., upper- and lower-most occurrences) of *D. purpurea* in streams in 2003 coincides roughly with its spatial extent along roads; however, the distribution of *D. purpurea* along streams was different from its distribution along the road network. In other words, *D. purpurea* did not occur in all stream segments downgradient of roads where

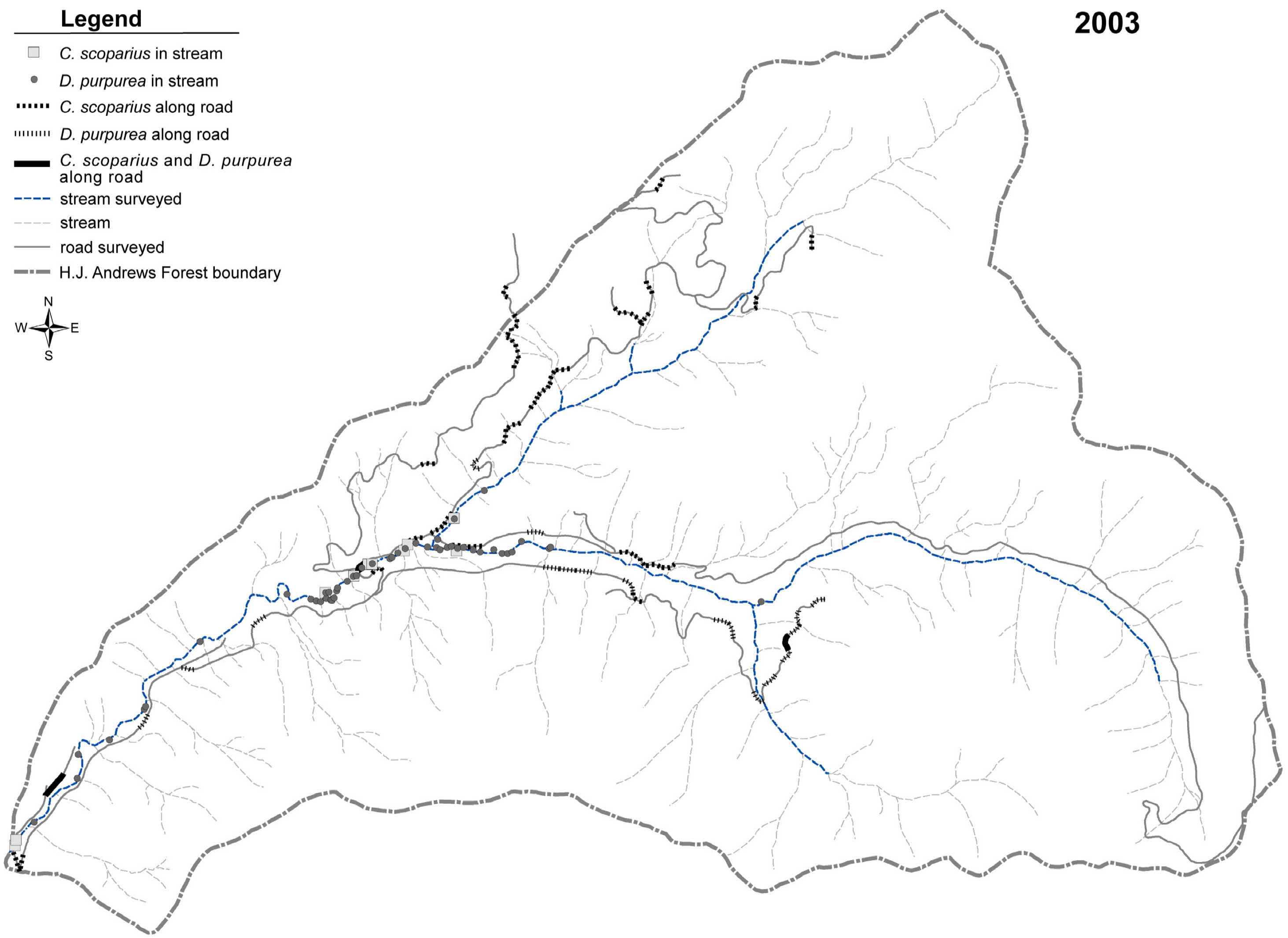

Figure 7. Map of *Cytisus scoparius* and *Digitalis purpurea* occurrences along roads and streams surveyed in 2003

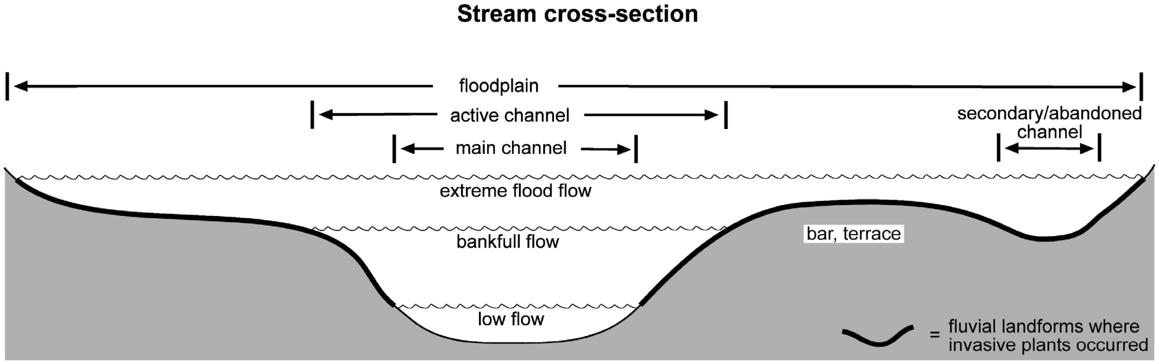

Figure 8. Schematic illustration of a stream channel cross-section showing fluvial landforms where *Cytisus scoparius* and *Digitalis purpurea* occurred in 2003 and stream feature terminology.

D. purpurea was present, nor did all in-stream locations of *D. purpurea* have adjacent seed sources along roads.

Both *C. scoparius* and *D. purpurea* occurred most frequently and in greatest abundance in the middle reaches of Lookout Creek and in lower McRae Creek where interactions between the road and stream network are also most common. However, at their uppermost extent in the stream network, both species tended to occur at sites where the stream is away from the road network and where forest separates the stream from road interaction.

The most upstream occurrence of *C. scoparius* in Lookout Creek was approximately 320 m upstream of the confluence of McRae and Lookout creeks where Road 1506 is very near the stream. The establishment of a *C. scoparius* patch at this location is likely a result of seeds dispersed directly from the adjacent road where *C. scoparius* has been present since 1994, or alternatively may be a relict patch which established at this site after it was clear-cut in 1971 (F. Swanson, personal communication). Five *C. scoparius* patches occurred along Lookout Creek, from approximately 220 m downstream of the McRae-Lookout junction to about 410 m downstream of the Road 1506 crossing of Lookout Creek (concrete bridge). This reach where *C. scoparius* was most frequent in 2003 is located immediately downstream of where a 1996 debris slide occurred. This debris slide occurred in a 1988 clear-cut where *C. scoparius* was likely present since before 1996 and where it was abundant by 2002. The slide moved onto and

Figure 9. Map of *Cytisus scoparius* distribution along roads and streams in the Andrews since 1994 with 1996 geomorphic disturbances. Figure shows the results of road and stream surveys in 2003 with results from road surveys conducted in 1994 (Parendes unpublished data) and 2002 (Cilenti unpublished data) and debris flow paths from 1996 (Snyder unpublished data).

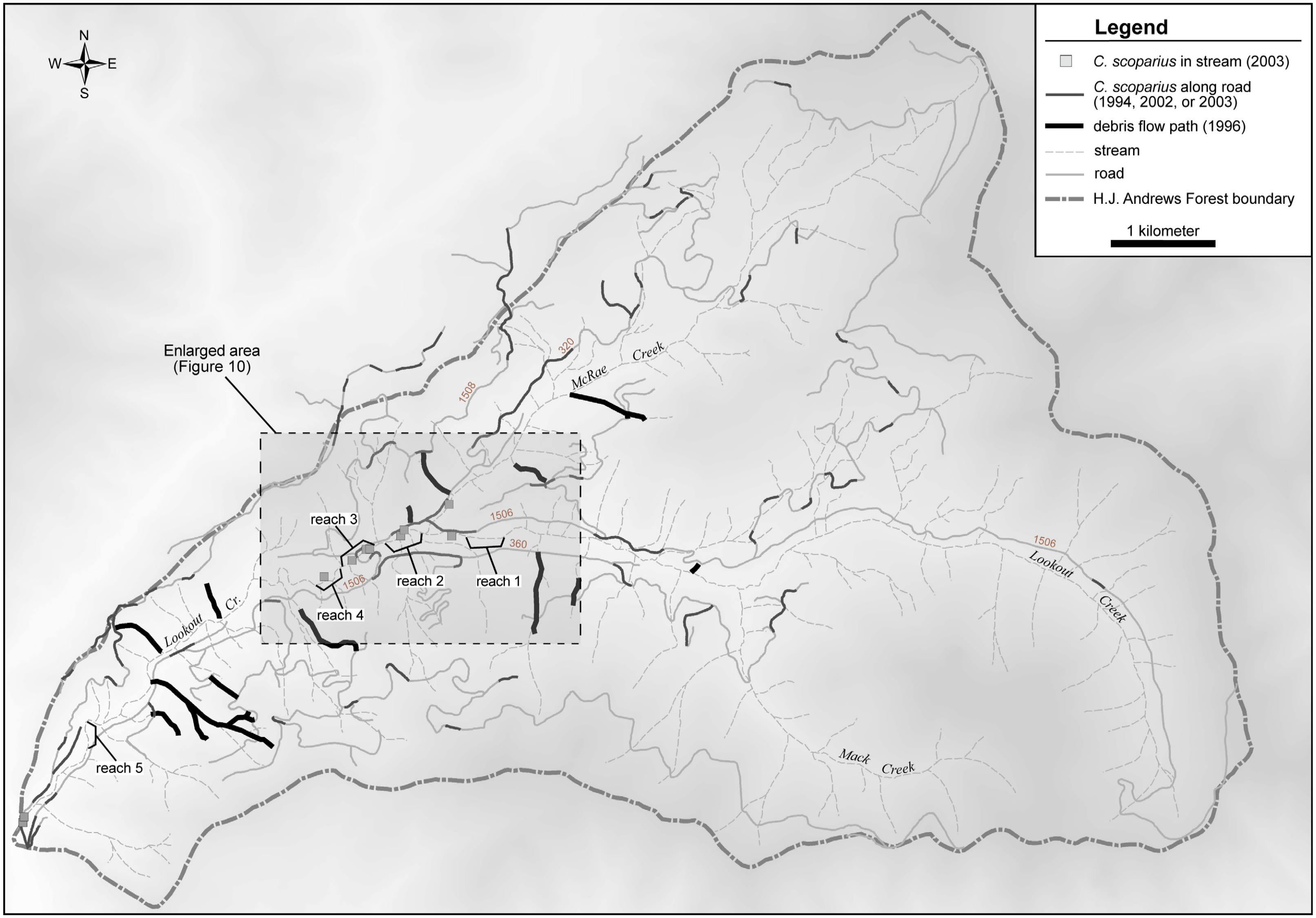
N
W
E
S
Legend
C. scoparius in stream (2003)
C. scoparius along road (1994, 2002, or 2003)
debris flow path (1996)
stream
road
H.J. Andrews Forest boundary
1 kilometer
Enlarged area (Figure 10)
1508
320
McRae Creek
1506
360
reach 1
reach 2
reach 3
reach 4
reach 5
1506
Lookout Cr.
1506
Lookout Creek
Mack Creek

Figure 9.

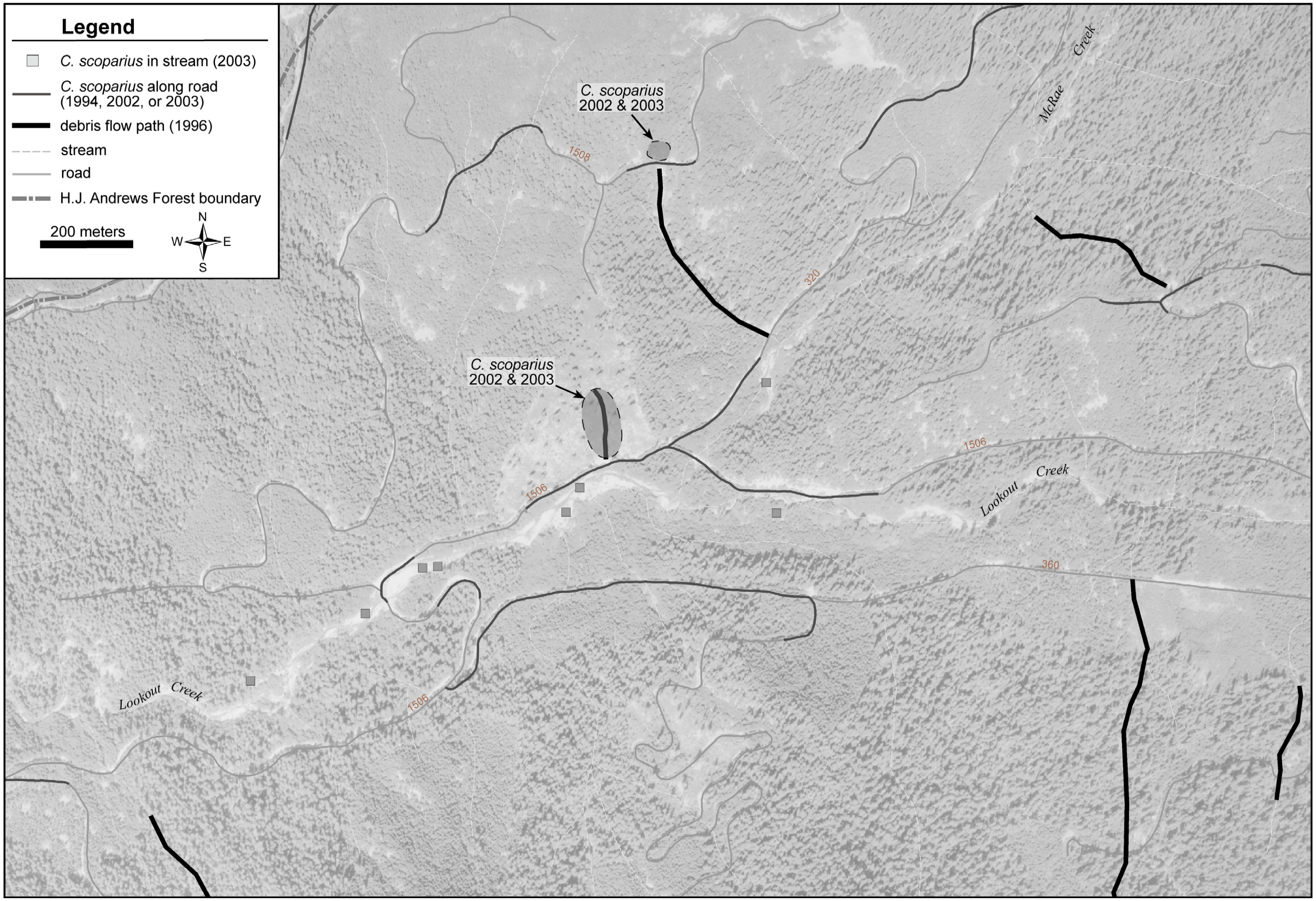

Figure 10. Enlarged view of *Cytisus scoparius* distribution in the vicinity of the McRae-Lookout creek junction since 1994.

Figure 11. Map of *Digitalis purpurea* distribution along roads and streams in the Andrews 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).

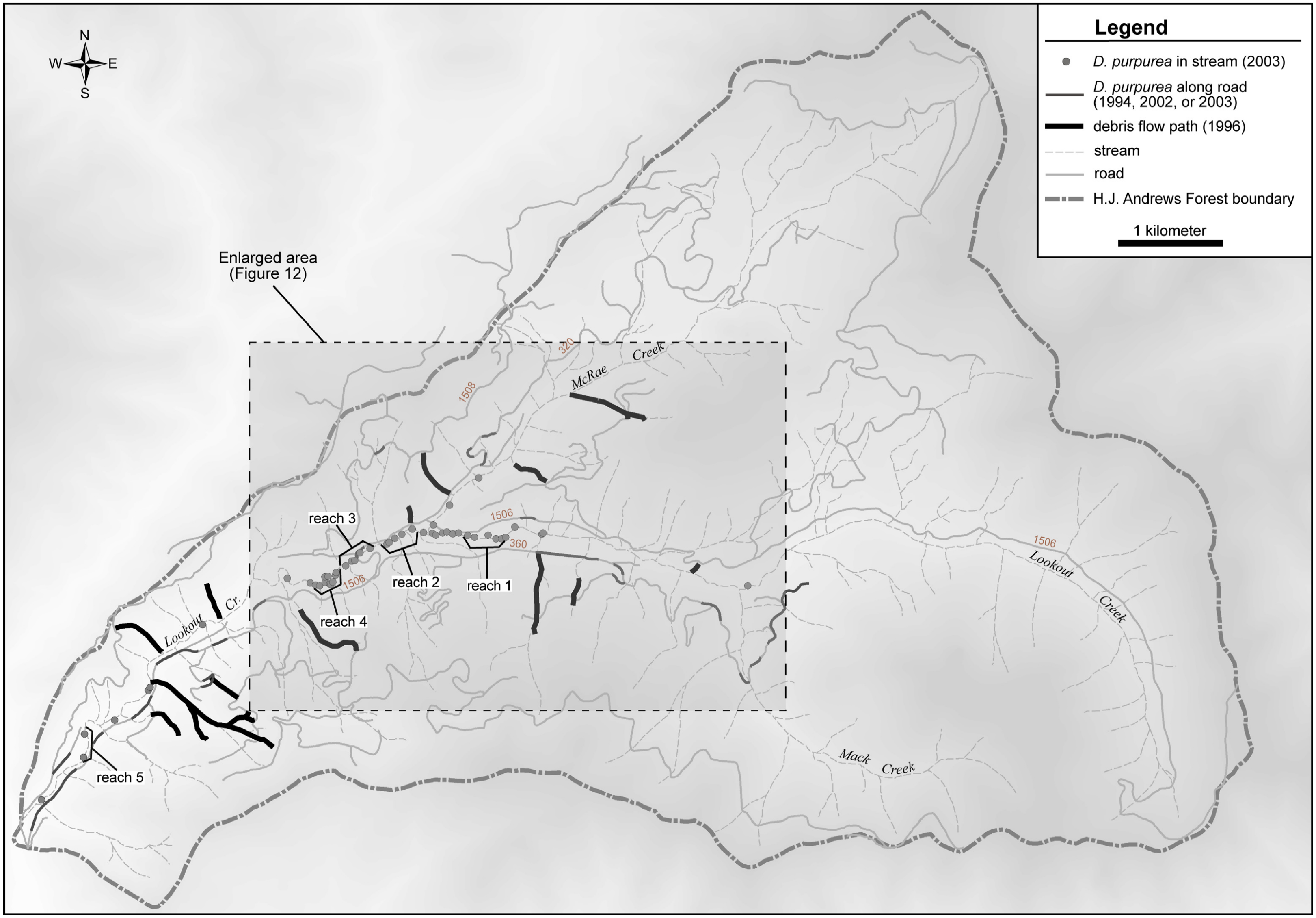
N
W
E
S
Legend
● *D. purpurea* in stream (2003)
D. purpurea along road (1994, 2002, or 2003)
debris flow path (1996)
stream
road
H.J. Andrews Forest boundary
1 kilometer
Enlarged area (Figure 12)
McRae Creek
320
1508
1506
360
reach 1
reach 2
reach 3
reach 4
reach 5
Lookout Cr.
Lookout Creek
Mack Creek

Figure 11.

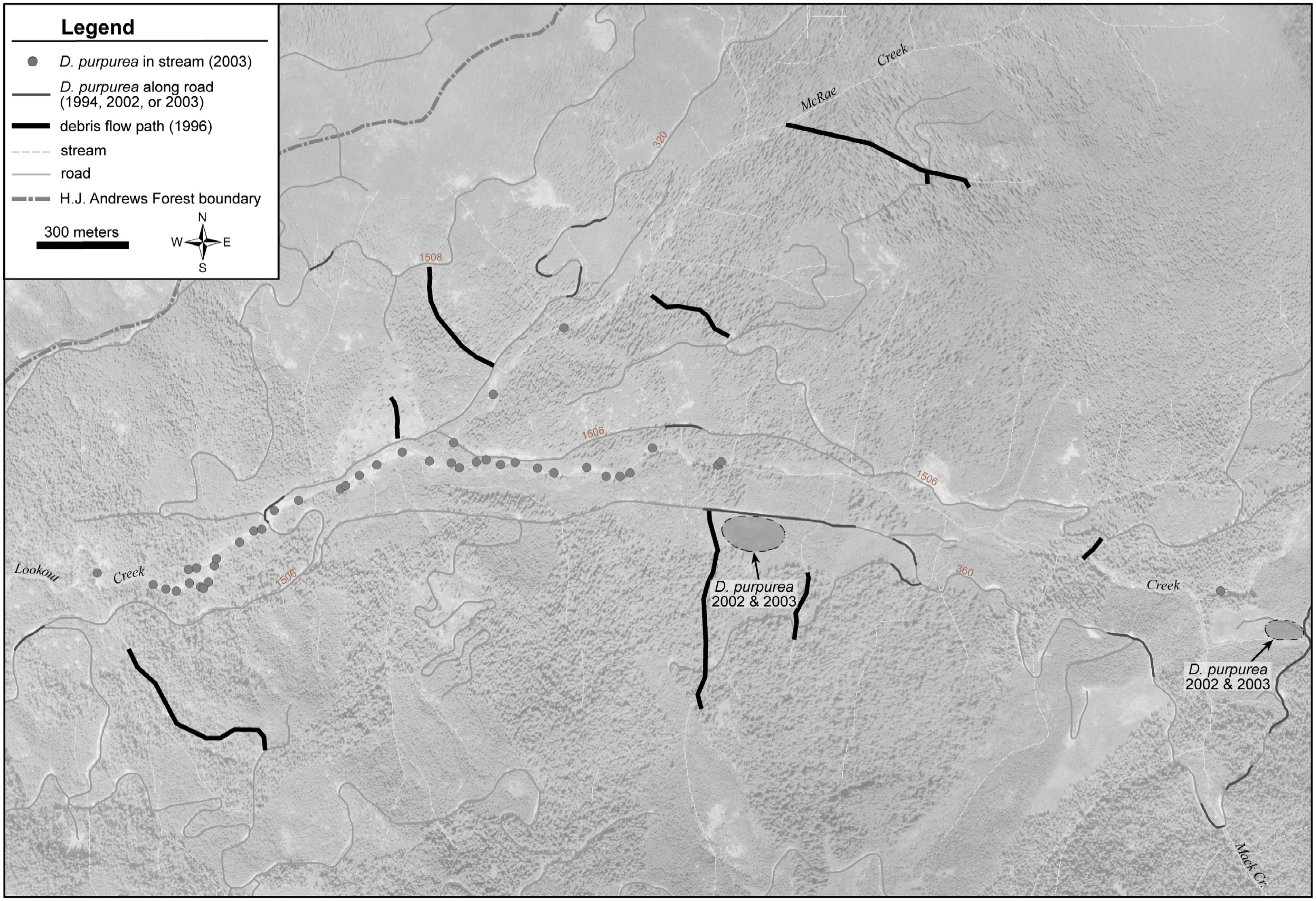

Figure 12. Enlarged view of *Digitalis purpurea* distribution in the vicinity of the McRae-Lookout creek junction since 1994.

across Road 1506 where *C. scoparius* was present since at least 1994 and deposited material on the road and near or in Lookout Creek here. Furthermore, Road 1506 is near Lookout Creek and crosses Lookout Creek at the "concrete bridge" in this reach (Figures 9 and 10). Two additional *C. scoparius* patches were located several kilometers downstream along Lookout Creek near the entrance to the Andrews, approximately 230 m upstream of the confluence of Lookout Creek and Blue River at low flow. In this area water is seasonally backed up from the Blue River Reservoir, and *C. scoparius* patches were located near the high-water mark for the reservoir and approximately 25 m from the highway (Figures 9). These patches are likely a result of seed dispersal from the adjacent highway.

In McRae Creek, the most upstream patch occurred about 450 m upstream of the junction with Lookout Creek, just downgradient of a tributary channel where a large debris flow occurred in 1996, and which crossed sections of roads 1508 and 320 along which *C. scoparius* was present in 2002 and 2003 (Figures 9 and 10). This large debris flow initiated upgradient at Road 1508 where *C. scoparius* had become established by 2002 on the road cutslope. Although not mapped in 1994 or 2002 by Parendes or Cilenti, this *C. scoparius* patch occurred more than 2 m from the road edge and as a result would not have been included in the road surveys in 1994 and 2002. At this location, McRae Creek is away from the road and separated by conifer forest.

D. purpurea had been present along Road 360 since 1994 and by 2003 it was very abundant along much of Road 360 and in two adjacent harvest patches. These two clear-cuts were harvested in 1985 and used for a stand replacement study during the 1980s, which also included sites in the Oregon Coast Range, where *D. purpurea* is abundant (S. Radosevich, personal communication; B. Bond, personal communication). *D. purpurea* was mapped along Road 360 near the upper clear-cut in 1994, but was not mapped at the lower clear-cut (Figure 4). Nevertheless, it was probably present in both clear-cuts since the time of the stand replacement study in the 1980s, but was not mapped near the lower clear-cut until 2002 because it did not occur within the 2-m road buffer used in the road surveys. At its upstream extent in Lookout Creek, *D. purpurea* occurred downgradient, but separated by distance (>150 m) and forest from seed sources on the hillslope in the upper clear-cut and along Road 360 where *D. purpurea* was present since before the 1996 flood (Figure 12). The long distance and tall trees separating the stream from seed source areas at this site make wind dispersal of seeds to this site unlikely. Rather, seeds were most likely transported into the stream here by overland flow or by way of flow along Road 360 that drains to the northeast in this area and which eventually contribute flow to a tributary channel that enters Lookout Creek approximately 350 m upstream of where *D. purpurea* occurred in Lookout Creek in 2003 (Figure 12).

However, most *D. purpurea* were found not below the potential source, but instead further downstream in the middle reaches of Lookout Creek below the entry point of a tributary channel where a large debris flow occurred in 1996. This debris flow crossed Road 360 and ran along a clear-cut where *D. purpurea* was likely present since before 1996. Lookout Creek is away (>150 m) from the road network at this site and remains away from any roads for approximately 800 m downstream. *D. purpurea* occurred relatively continuously through this reach and below for 3 km where *D. purpurea* was generally absent from the road (Figures 11 and 12).

D. purpurea was uncommon in the McRae Creek drainage. The farthest upstream location of *D. purpurea* in McRae Creek was downgradient of the highest upslope seed source along a road, at the base of a tributary channel and downgradient but also separated by distance and forest from road seed sources. Two *D. purpurea* patches occurred in McRae Creek below this point to the confluence with Lookout Creek (Figures 11 and 12). Of 49 *D. purpurea* patches observed in streams, 46 occurred in Lookout Creek; 38 (78%) were observed in a 3.1-km reach of Lookout Creek stretching from approximately 1.4 km upstream of the McRae-Lookout junction to about 1 km downstream of the Road 1506 “concrete bridge” crossing. Only seven *D. purpurea* patches with 29 plants occurred in the lower 4.9 km of Lookout Creek. Two patches in lower Lookout Creek were located where a large debris flow deposit existed in 1996 (Figure 11).

Plant distributions at the stream reach scale

C. scoparius tended to occur on established floodplain terraces in wide alluvial reaches of the stream network whereas *D. purpurea* was commonly found along stream margins in secondary high-water channels or areas that had been abandoned by the main channel. Five stream reaches where *C. scoparius* and *D. purpurea* were most abundant in the summer of 2003 have experienced avulsions of the main channel between 1990 and 2003 (Figures 13 to 17). *C. scoparius* was most often found in open patches of dry fine-grained substrate where light levels were high. *D. purpurea* occurred almost exclusively in coarser-grained substrate, most often on cobble or boulder bars with sandy matrices where light levels were also high. Both species generally occurred in stream sites protected from scour, immediately up or downstream from obstructions like large wood, boulders, or vegetation (Figures 13 to 19).

Reach 1

Above the confluence of McRae Creek with Lookout Creek in Reach 1 (Figures 9 and 11), the unvegetated floodplain area expanded markedly between the fall of 1990 and fall of 1996 (Figure 13). In 1990 the stream corridor was narrow and historical discharges in Lookout Creek were relatively low during the period 1990 to 1996 (Figure 4). Widening occurred in 1996. By 2000, vegetation had colonized parts of the floodplain that had been scoured in 1996, but large areas remained exposed in the summer of 2003. *C. scoparius* was absent from this section of the stream, but *D. purpurea* patches were mainly in areas had been occupied by the main channel in 1990 or 1996 (Figure 13), and appeared to be secondary high-water channels in 2003. In most cases, the channel appears to have avulsed in the winter of 1996. *D. purpurea* patches are located at sites where local channel obstructions (e.g., large wood jams, stumps, standing vegetation) may have deflected flows and provided local refuge from scouring processes (Figures 13 and 18).

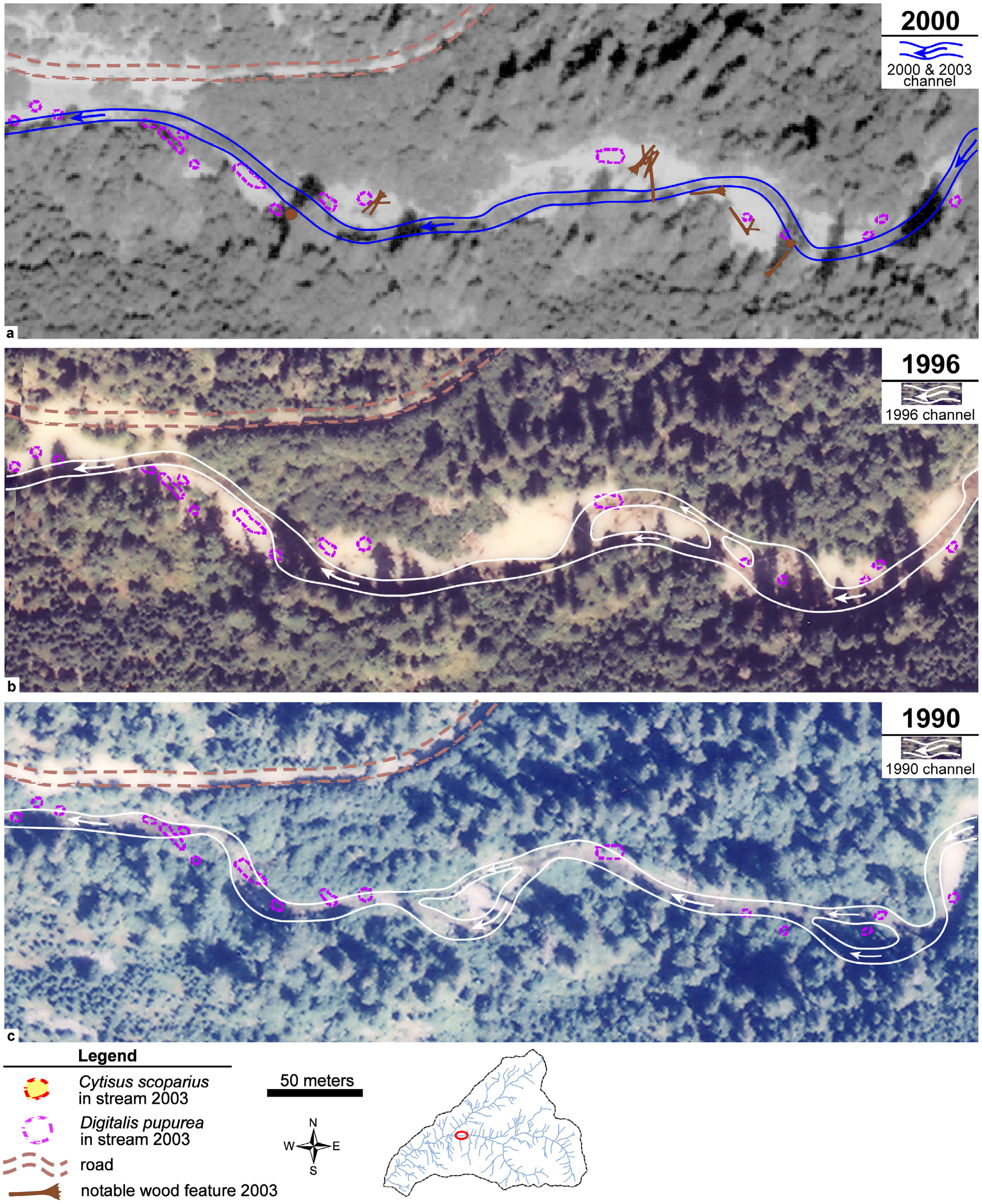

Figure 13. Reach 1 in Lookout Creek upstream of the McRae-Lookout creek junction. Locations of *Cytisus scoparius* and *Digitalis purpurea* patches in 2003 are overlain on aerial photographs from summer of 1990, 1996, and 2000. (a) Aerial photograph from 2000 shows the low-flow channel in 2000 interpreted from aerial photograph and the low-flow channel in 2003 from field observation. Note the location of major wood features observed in 2003. (b) Aerial photograph from 1996 shows the post-flood low-flow channel in 1996 interpreted from aerial photograph. (c) Aerial photograph from 1990 shows the pre-1996 flood low-flow channel interpreted from aerial photograph.

Reach 2

Reach 2 in Lookout Creek below the McRae Creek confluence (Figures 9 and 11) was also considerably widened during 1996 (Figure 14). This was one of the widest parts of Lookout Creek in 1996 and remained wide through 2000 with only modest vegetation encroachment by 2003. As a result of flooding in 1996 (Wondzell and Swanson 1999) and subsequent reworking during floods that occurred in 1999 and 2000, very little of the main channel from 1990 remained active in 2000. The main channel did not shift noticeably between 2000 and 2003. This reach had the highest abundance of *C. scoparius* and *D. purpurea* in the stream network.

C. scoparius occurred at two sites in Reach 2, both of which appear to have been well isolated from the active channel since 1996 and perhaps even earlier (Figure 14). The upstream *C. scoparius* site was located on the inside of a large channel bend and was elevated by over 1.5 m above the low flow channel. The largest *C. scoparius* patch observed in the streams in 2003 was located downstream among other vegetation and below two small logs on a broad sandy area of the floodplain, approximately 20 m laterally from the low flow channel (Figures 14 and 19). This site appears to have been particularly isolated from flood scour since between 1996 and 2003. In the upper section of Reach 2, *D. purpurea* was most abundant in 2003 in secondary channels that were abandoned during flood events in 1996 and 1998 (Figure 14). No specific channel feature was observed in 2003 to which channel redirection can be attributed, but most of the plants present in 2003 were located in a secondary channel now separated from the main channel by an elevated cobble bar (Figure 18). Because of this obstruction, flows that have entered this secondary channel during post-1998 high-water events may have been moderate enough to allow seed deposition without eliminating established plants. Further downstream in the middle section of Reach 2, *D. purpurea* patches appeared to be related to local obstructions perhaps responsible in part for directing flow and providing protection from scouring (Figures 14 and 18).

Figure 14. Reach 2 in Lookout Creek immediately downstream of the McRae-Lookout creek junction. Locations of *Cytisus scoparius* and *Digitalis purpurea* patches in 2003 are overlain on aerial photograph images from summer of 1990, 1996, and 2000. (a) Aerial photograph from 2000 shows the low-flow channel in 1998 interpreted from color-infrared aerial photograph, the low-flow channel in 2000 interpreted from aerial photograph, and the low-flow channel in 2003 from field observation. Note the location of major wood features observed in 2003. (b) Aerial photograph from 1996 shows the post-flood low-flow channel in 1996 from Wondzell and Swanson (1999) and interpreted from aerial photograph. (c) Aerial photograph from 1990 shows the pre-1996 flood low-flow channel from Wondzell and Swanson (1999) and interpreted from aerial photograph.

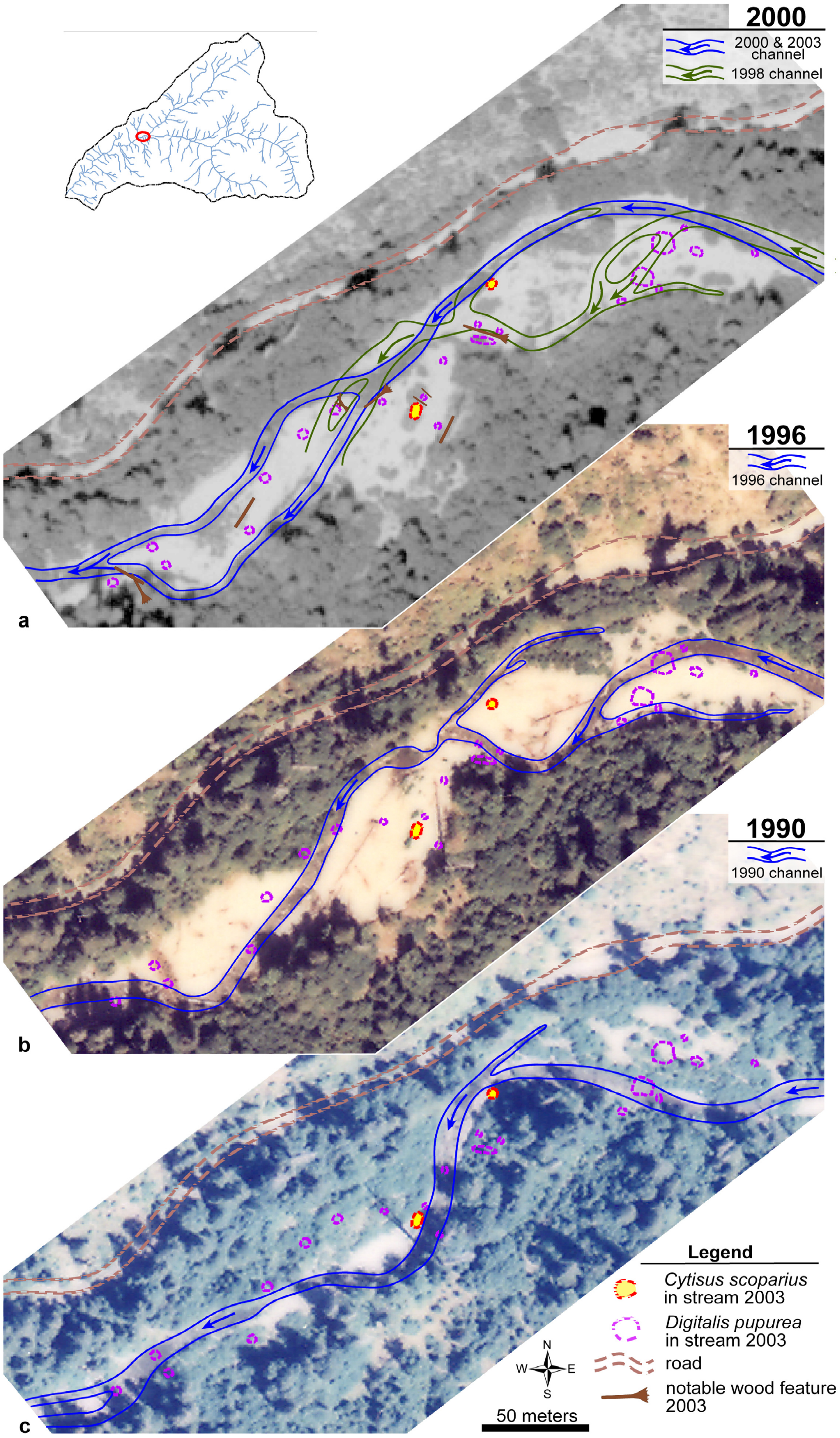
2000
2000 & 2003 channel
1998 channel
a
1996
1996 channel
b
1990
1990 channel
c
Legend
Cytisus scoparius in stream 2003
Digitalis pupurea in stream 2003
road
notable wood feature 2003
N
W
E
S
50 meters

Figure 14.

Reach 3

Reach 3 is located approximately 500 m downstream of Reach 2, in the vicinity of the Road 1506 concrete bridge (Figures 9 and 11). Similar to some other reaches with large invasive plant populations, this reach experienced substantial scouring of vegetation in 1996 and most of this area remained uncolonized through 2000 and 2003. The active channel of Lookout Creek has moved across much of the unvegetated floodplain since 1990. In the summer of 2003, three patches of *C. scoparius* and five patches of *D. purpurea* were observed in this reach of Lookout Creek (Figure 15). *C. scoparius* and *D. purpurea* patches observed in 2003 were in exposed areas.

At the northeast (upstream) end of Reach 3 near where several *C. scoparius* sites were located, the channel appears to have maintained its course between 1998 and 2003 (Figure 15). Two *C. scoparius* sites here were found nestled in flood-scour protected areas amongst large wood and debris jams (Figures 15 and 19). Just above the bridge *D. purpurea* patches occurred in secondary channels where the main channel existed in 1996 and 1998. A large *D. purpurea* patch was located below a debris deposit in a secondary channel occupied by the main channel in 1996. Other sites in this area also appeared to be locally protected from flood scouring by positions of logs and wood debris (Figures 15 and 18). Immediately downstream of the bridge the channel position shifted very little between 1996 and 2003. *D. purpurea* in 2003 was most abundant in a secondary channel (in the southwest corner of Figure 15) that apparently was abandoned during the 1996 flood. As of 2003 this channel was separated from the active channel by a cobble bar and debris jam at its entrance (Figures 15 and 18). One patch of *C. scoparius* and several additional patches of *D. purpurea* were located elsewhere in this reach in locations where channels existed in 1990 or 1996, but which in 2003 were protected from flood scouring by large wood deposits on the north side of the main channel and bridge riprap on the south side.

Figure 15. Reach 3 in Lookout Creek at the Road 1506 "concrete bridge". Locations of *Cytisus scoparius* and *Digitalis purpurea* patches in 2003 are overlain on aerial photograph images from summer of 1990, 1996, and 2000. (a) Aerial photograph from 2000 shows the low-flow channel in 1998 interpreted from color-infrared aerial photograph, the low-flow channel in 2000 interpreted from aerial photograph, and the low-flow channel in 2003 from field observation. Note the location of major wood features observed in 2003. (b) Aerial photograph from 1996 shows the post-flood low-flow channel in 1996 interpreted from aerial photograph and low-elevation blimp photographs. (c) Aerial photograph from 1990 shows the pre-1996 flood low-flow channel interpreted from aerial photograph.

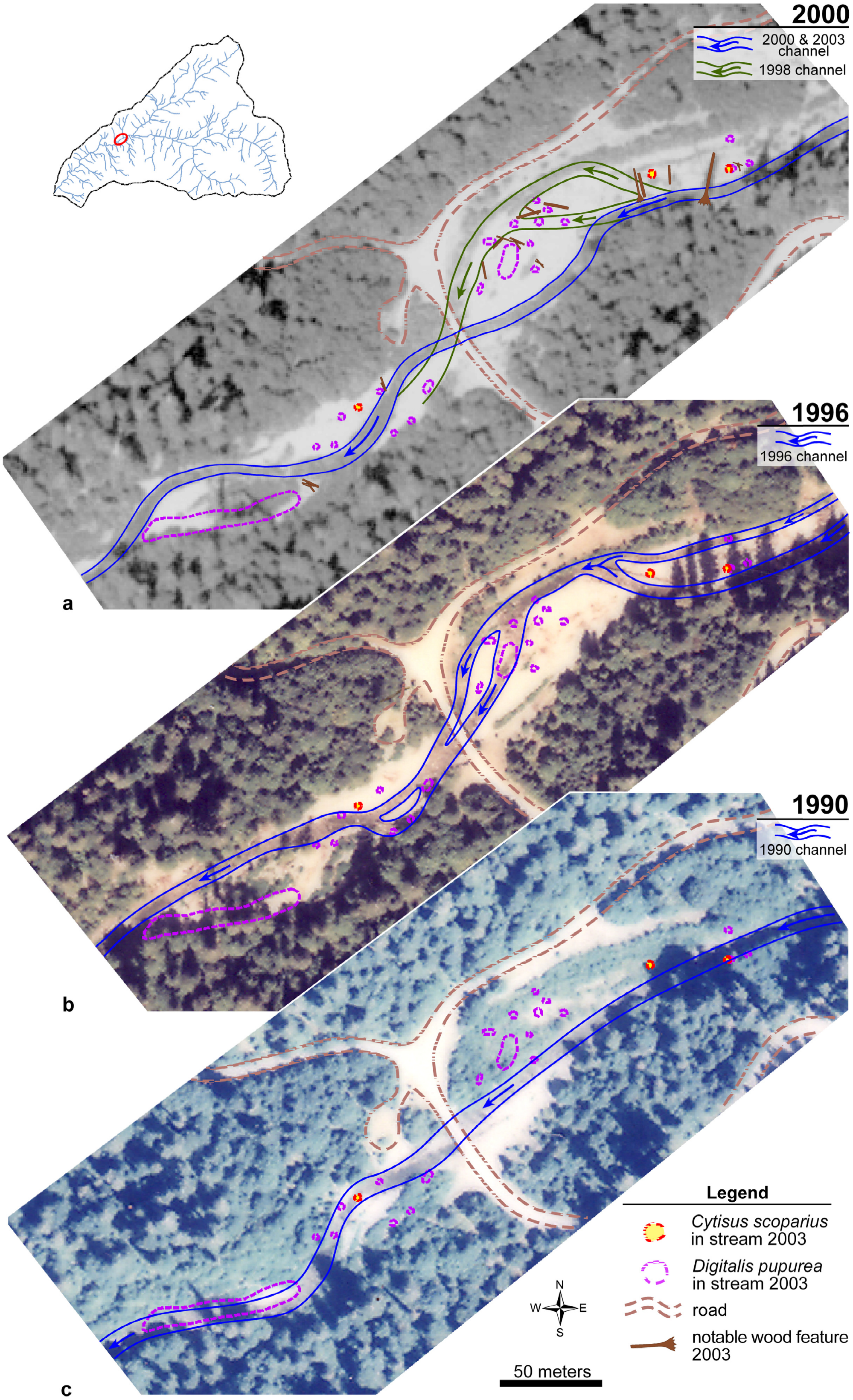
2000
2000 & 2003 channel
1998 channel
a
1996
1996 channel
b
1990
1990 channel
c
Legend
Cytisus scoparius in stream 2003
Digitalis pupurea in stream 2003
road
notable wood feature 2003
N
W
E
S
50 meters

Figure 15.

Reach 4

Further downstream approximately 300 m below the concrete bridge (Figures 9 and 11), the 2003 channel splits into three channels separated by large wood deposits in and along the stream channel (Figure 16). Here the exposed floodplain in 1996 and 2000 was lower than at reaches in the vicinity of the bridge and in the reach below McRae Creek. Patches of *C. scoparius* and *D. purpurea* here appeared to be closely associated with the locations of large wood deposits (Figure 16). Flood scouring since 1990 has noticeably widened the unvegetated floodplain in parts of the reach. Much of this widening can be attributed to flooding in 1996, but the lower (western) section of this reach was widened most after 1996. A large patch of *D. purpurea* was observed in 2003 in this area where the channel shifted between 1996 and 2000. *D. purpurea* was present along a secondary channel in this reach. As of 2003 this area was protected by a large wood jam upstream (Figure 16). *C. scoparius* and *D. purpurea* were relatively uncommon in Lookout Creek below this reach.

Reach 5

In lower Lookout Creek at Reach 5, located approximately 4.5 km downstream of the concrete bridge (Figures 9 and 11), flooding in 1996 removed vegetation, widening this reach, and configured the main channel into a single thread through the upper section of the reach (Figure 17). The position of the main channel changed very little between 1996 and 2003. A patch of *D. purpurea* was found at the head of the reach where the active channel was braided in 1990. This patch was on an elevated cobble bar or terrace, protected by a log with several plants located on fine sediment in a flood-scour protected depression (Figures 17 and 18). Another *D. purpurea* patch was located on a cobble bar downstream of two constricting bedrock outcroppings and just upstream of a very large debris jam that pools water at the downstream end of this reach (shown in bottom of Figure 17). These features appear to protect this lower site from scouring flows.

Figure 16. Reach 4 in Lookout Creek downstream of the Road 1506 "concrete bridge." Locations of *Cytisus scoparius* and *Digitalis purpurea* patches in 2003 are overlain on aerial photograph images from summer of 1990, 1996, and 2000. (a) Aerial photograph from 2000 shows the low-flow channel in 2000 interpreted from aerial photograph and the low-flow channel in 2003 from field observation. Note the location of major wood features observed in 2003. (b) Aerial photograph from 1996 shows the post-flood low-flow channel in 1996 interpreted from aerial photograph and low-elevation blimp photographs. Dashed channel outline represents unconfirmed channel course. (c) Aerial photograph from 1990 shows the pre-1996 flood low-flow channel interpreted from aerial photograph.

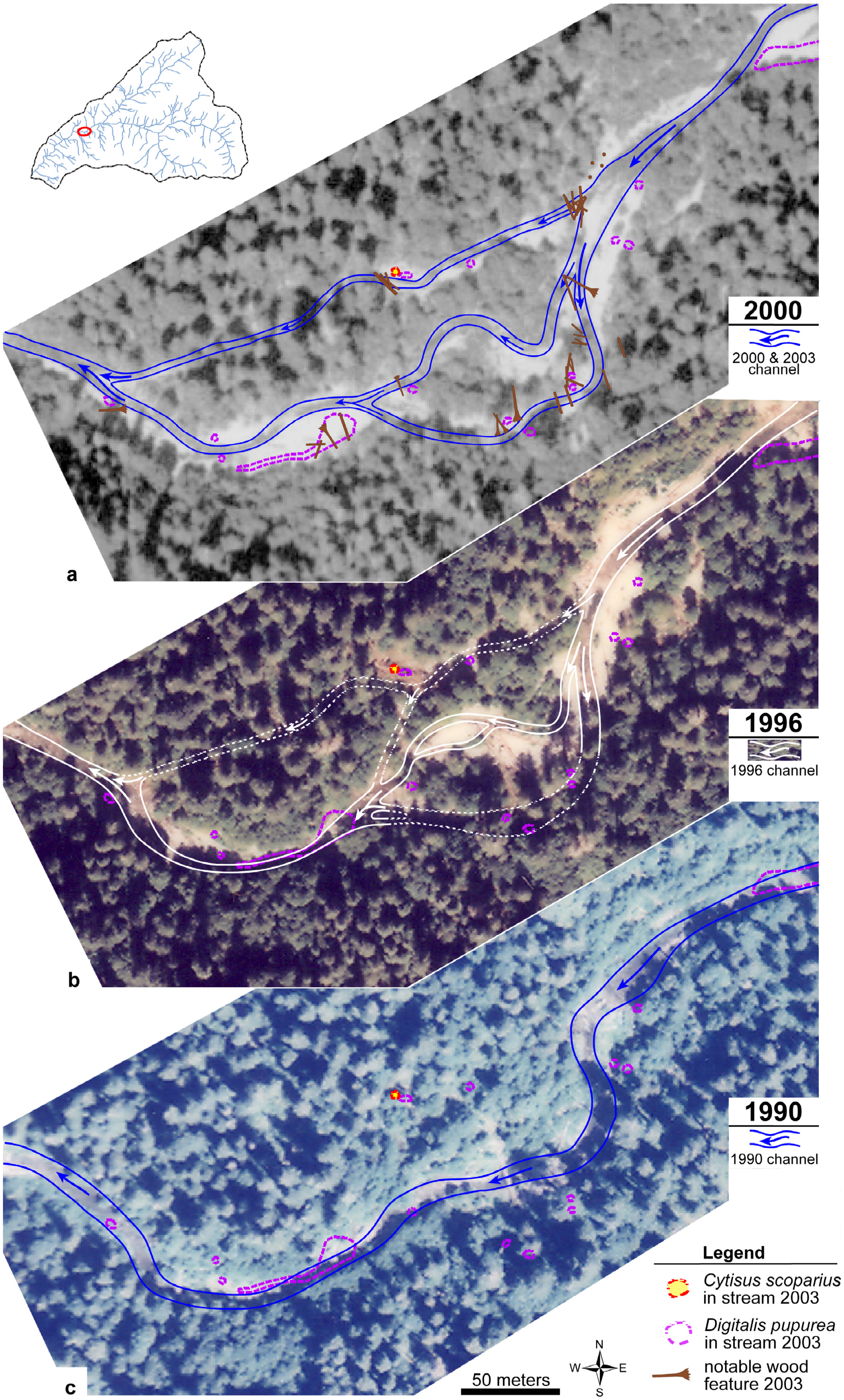
2000
2000 & 2003 channel
a
1996
1996 channel
b
1990
1990 channel
c
Legend
Cytisus scoparius in stream 2003
Digitalis pupurea in stream 2003
notable wood feature 2003
50 meters
N
W
E
S

Figure 16.

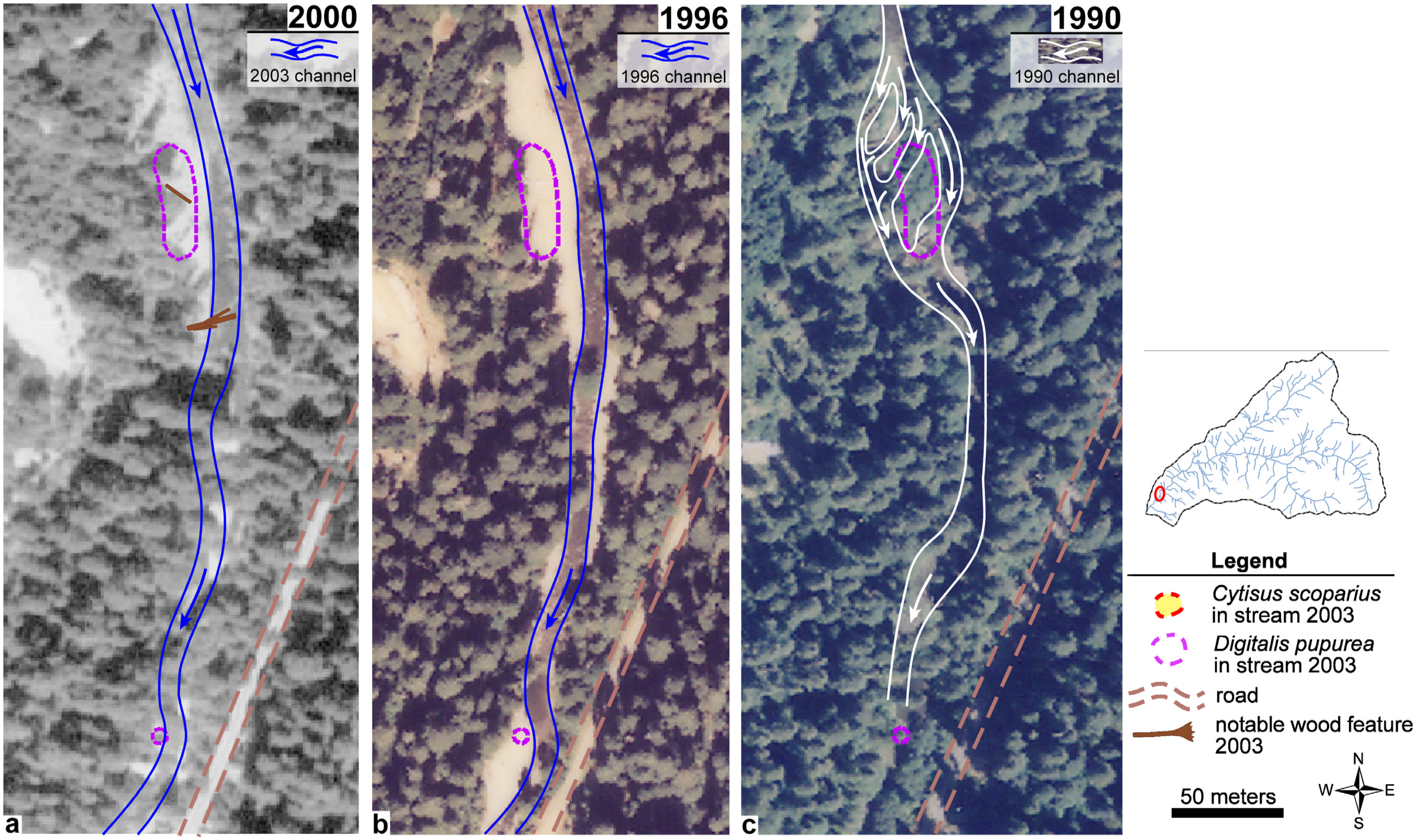

Figure 17. Reach 5 in lower Lookout Creek. Locations of *Digitalis purpurea* patches in 2003 are overlain on aerial photograph images from summer of 1990, 1996, and 2000. (a) Aerial photograph from 2000 shows the low-flow channel in 2003 from field observation. Note the location of major wood features observed in 2003. (b) Aerial photograph from 1996 shows the post-flood low-flow channel in 1996 from Faustini (2000) and interpreted from aerial photograph. (c) Aerial photograph from 1990 shows the pre-1996 flood low-flow channel from Nakamura and Swanson (1993).

Figure 18 (a–g). Typical stream sites where *Digitalis purpurea* occurred in 2003. (a) View roughly down secondary channel in Lookout Creek at Reach 2 (immediately below McRae-Lookout junction). (b) View up secondary channel in Reach 2 [opposite direction of photo in (a)]. (c) Close-up view of *Digitalis purpurea* plant in cobble-boulder niche in secondary channel at Reach 2. High flow is from top to bottom of image. (d) View roughly up secondary channel in Lookout Creek at Reach 1 (above McRae-Lookout junction). Note large wood debris jam upstream blocking entrance to channel. (e) Close-up view of *Digitalis purpurea* plant in cobble niche in Lookout Creek above McRae-Lookout junction. High flow is from upper left to lower right in image. (f) View roughly up secondary channel in Lookout Creek at Reach 3 (at "concrete bridge"). Note debris jam upstream of *Digitalis purpurea* present in foreground of image. (g) Close-up view of *Digitalis purpurea* in cobble niche at lower section of Reach 3. High flow is from upper left to lower right in image.

Figure 18 (h–n). Typical stream sites where *Digitalis purpurea* occurred in 2003 (Continued). (h) View roughly upstream on island in Lookout Creek above McRae-Lookout junction. Note large log directly upstream of *Digitalis purpurea* plant in foreground of image. (j) View roughly upstream on island in Lookout Creek located upstream of McRae-Lookout junction. Note wood debris upstream of *Digitalis purpurea* in foreground of image. (k) View roughly upstream on bar/terrace in lower Lookout Creek at Reach 5. Note *Digitalis purpurea* in foreground of image located on fine substrate in a protected depression. High flow is from upper left to lower right in image. (l) View roughly up secondary channel in Lookout Creek at lower Reach 3/upper Reach 4. Note *Digitalis purpurea* in fine substrate. (m) View up secondary channel in Lookout Creek at Reach 2. Note *Digitalis purpurea* in fine substrate at channel margin. (n) View across secondary channel at Reach 2. Note *Digitalis purpurea* located in fine substrate downstream of large log.

Figure 19. Typical stream sites where *Cytisus scoparius* occurred in 2003. (a) View roughly downstream on floodplain in Lookout Creek at Reach 2. Note *Cytisus scoparius* on fine substrate. (b) View roughly upstream on bar/terrace in Lookout Creek at upper Reach 3. Note *Cytisus scoparius* located downstream of debris in fine substrate. (c) View roughly upstream on bar/terrace in Lookout Creek at lower Reach 3. Note large fraction of fines substrate in matrix of cobble bar.

Geomorphology and plant distributions

In the Andrews, valley morphology strongly controls stream channel and floodplain characteristics. The floodplain is typically wider in low-gradient unconstrained reaches, and broad valleys in Lookout Creek generally have young, wide floodplains with many secondary channels (Grant and Swanson 1995). In 2003, *C. scoparius* and *D. purpurea* tended to occur in low-gradient unconstrained reaches of Lookout Creek with wide unvegetated floodplains.

Valley morphology

Cross-sectional profiles of valley shape at 31 approximately evenly spaced (~350 m) transects were generated from a 10-m resolution DEM and grouped according to presence or absence of *C. scoparius* and *D. purpurea* (Figure 20). These profiles show general similarity to valley morphology characteristics reported by *Grant and Swanson* (1995). Valley width measurements approximately between transects 13 and 14 and between transects 15 and 17 (Figure 20) averaged 112 m and 166 m respectively; the reach approximately from transect 14 to 15 has a lower average valley width of 59 m (Grant and Swanson 1995). A visual comparison of grouped profiles indicates that *C. scoparius* and *D. purpurea* most often occupied stream reaches through wide valleys, most notably the middle reach of Lookout Creek between transects 10 and 17 where the channel is relatively unconstrained by valley shape (Figure 20). Approximately below transect 17 to transect 21 the valley narrows, averaging a valley floor width of only 25 m (Grant and Swanson 1995). *D. purpurea* were markedly less common in Lookout Creek below transect 17 but also occurred downstream of transect 17, generally in reaches where the valley is wide. No stream-related occurrences of *C. scoparius* were observed below transect 17 (Figure 20).

Stream gradient

C. scoparius and *D. purpurea* patches in the Andrews stream network tended to occur mainly in areas of low-slope terrain and where stream gradient is low (Figure 21). Using the 10-m DEM, a longitudinal profile and stream gradient calculations were derived for 32 segments of Lookout Creek (below the uppermost *D. purpurea* source present along Road 360) between transects at intervals of approximately 350 m (Figure 20). These figures show that *C. scoparius* and *D. purpurea* patches were particularly frequent in and around the low-gradient, unconstrained reach of Lookout Creek approximately between transects 11 and 17 (Figure 21). *D. purpurea* was observed upstream in steeper sections of Lookout Creek, but was largely

Figure 20. Valley morphology along Lookout Creek and *Cytisus scoparius* and *Digitalis purpurea* distribution along roads and streams since 1994. Figure shows valley transect locations and profiles downstream of the uppermost *Digitalis purpurea* seed source along Road 360 (derived from a 10-m DEM). Results of road and stream surveys in 2003 are shown with road survey results from 1994 (Parendes unpublished data) and 2002 (Cilenti unpublished data) and debris flow paths from 1996 (Snyder unpublished data).

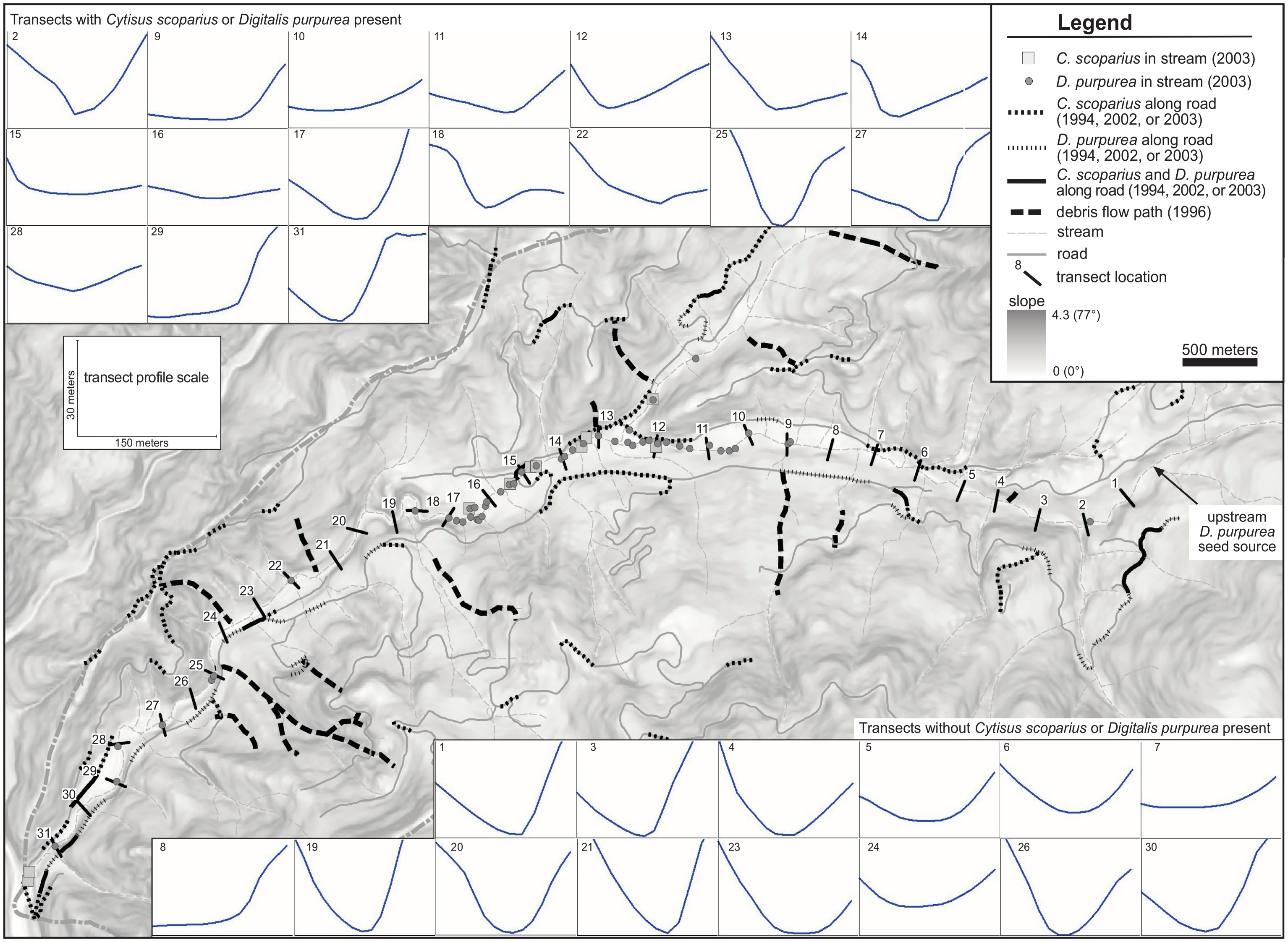
Transects with *Cytisus scoparius* or *Digitalis purpurea* present
2
9
10
11
12
13
14
15
16
17
18
22
25
27
28
29
31
Legend
C. scoparius in stream (2003)
D. purpurea in stream (2003)
C. scoparius along road (1994, 2002, or 2003)
D. purpurea along road (1994, 2002, or 2003)
C. scoparius and *D. purpurea* along road (1994, 2002, or 2003)
debris flow path (1996)
stream
road
8
transect location
slope
4.3 (77°)
0 (0°)
500 meters
transect profile scale
30 meters
150 meters
upstream *D. purpurea* seed source
Transects without *Cytisus scoparius* or *Digitalis purpurea* present
1
3
4
5
6
7
8
19
20
21
23
24
26
30

Figure 20.

absent downstream of transect 16 where stream gradient also increases. Farther downstream *D. purpurea* reappeared discontinuously, but was mostly restricted to low-gradient stream sections. *C. scoparius* occurred in Lookout Creek only between transects 11 and 17 (Figure 21).

C. scoparius occurred in 5 (16%) of 32 stream segments (*C. scoparius* patches near the Blue River confluence at the Andrews entrance were excluded because they were road-related occurrences). *C. scoparius* occurred in 2 (11%) of 19 stream segments where gradient is greater than 0.03 and occupied 3 (23%) of 13 stream segments with gradients below 0.03 (Table 5). *D. purpurea* occupied 17 (53%) of 32 stream segments. It occurred in 8 (42%) of 19 segments with gradients above 0.03 and 9 (69%) of 13 segments with gradients below 0.03 (Table 5). Patches of *C. scoparius* and *D. purpurea* observed in high-gradient stretches of Lookout Creek

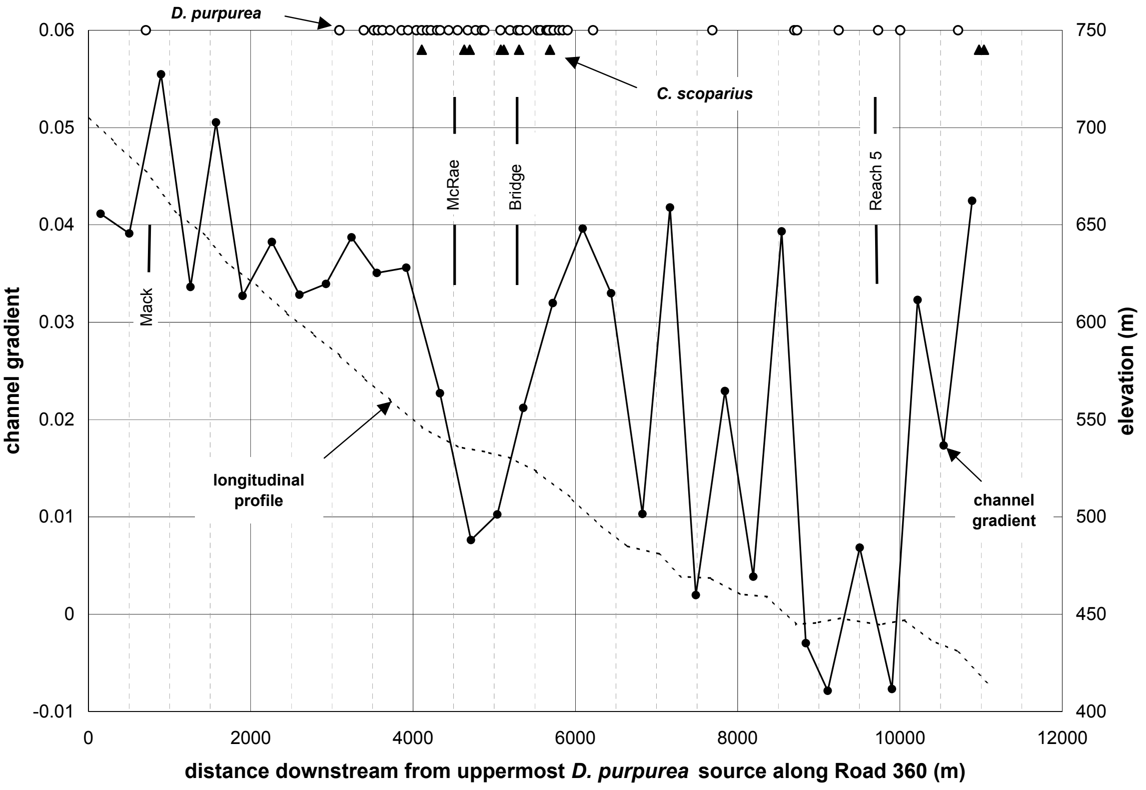

Figure 21. Stream gradient in Lookout Creek in relation to *Cytisus scoparius* and *Digitalis purpurea* distribution along streams in 2003. Figure shows stream gradient (primary y-axis) in Lookout Creek and the longitudinal stream profile (secondary y-axis) (derived from a 10-m DEM) downstream of the uppermost *Digitalis purpurea* seed source along Road 360 shown in Figure 20.

Table 5. *Cytisus scoparius* and *Digitalis purpurea* distribution by stream gradient

species	stream gradient	present	absent	all segments
Cytisus scoparius	<0.01	14% (1)	86% (6)	22% (7)
	0.01-0.019	33% (1)	67% (2)	9% (3)
	0.02-0.029	33% (1)	67% (2)	9% (3)
	0.03-0.039	15% (2)	85% (11)	41% (13)
	≥0.04	0% (0)	100% (6)	19% (6)
	total	**16% (5)**	**84% (27)**	**100% (32)**
Digitalis purpurea	<0.01	71% (5)	29% (2)	22% (7)
	0.01-0.019	67% (2)	33% (1)	9% (3)
	0.02-0.029	67% (2)	33% (1)	9% (3)
	0.03-0.039	54% (7)	46% (6)	41% (13)
	≥0.04	17% (1)	83% (5)	19% (6)
	total	**53% (17)**	**47% (15)**	**100% (32)**

were generally closely associated with large wood deposits or other features that have likely protected the site from scour (e.g., standing vegetation, large boulders, bedrock features).

Unvegetated floodplain width

In Lookout Creek, flooding in 1996 removed riparian vegetation (Johnson *et al.* 2000) and reworked channel sediment (Wondzell and Swanson 1999). The width of the unvegetated floodplain was measured from aerial photographs of 1994, 1996, and 2000 at transect locations with intervals of approximately 350 m (Figure 20). Aerial photographs were not available for more recent years. The area of the unvegetated floodplain along much of Lookout Creek increased markedly in 1996 and was widened further at some locations by flooding that occurred between 1996 and 2000 (Figure 22). There is a strong positive relationship between the width of the unvegetated floodplain in 1996 and 2000 and *C. scoparius* and *D. purpurea* frequency and abundance in Lookout Creek during the summer of 2003. Additionally, unvegetated floodplain width in 1996 and 2000 was roughly inversely related to stream gradient (Figures 21 and 22).

The greatest *D. purpurea* frequencies and abundances occurred in the low-gradient unconstrained reach of Lookout Creek where the unvegetated floodplain width in 1996 and

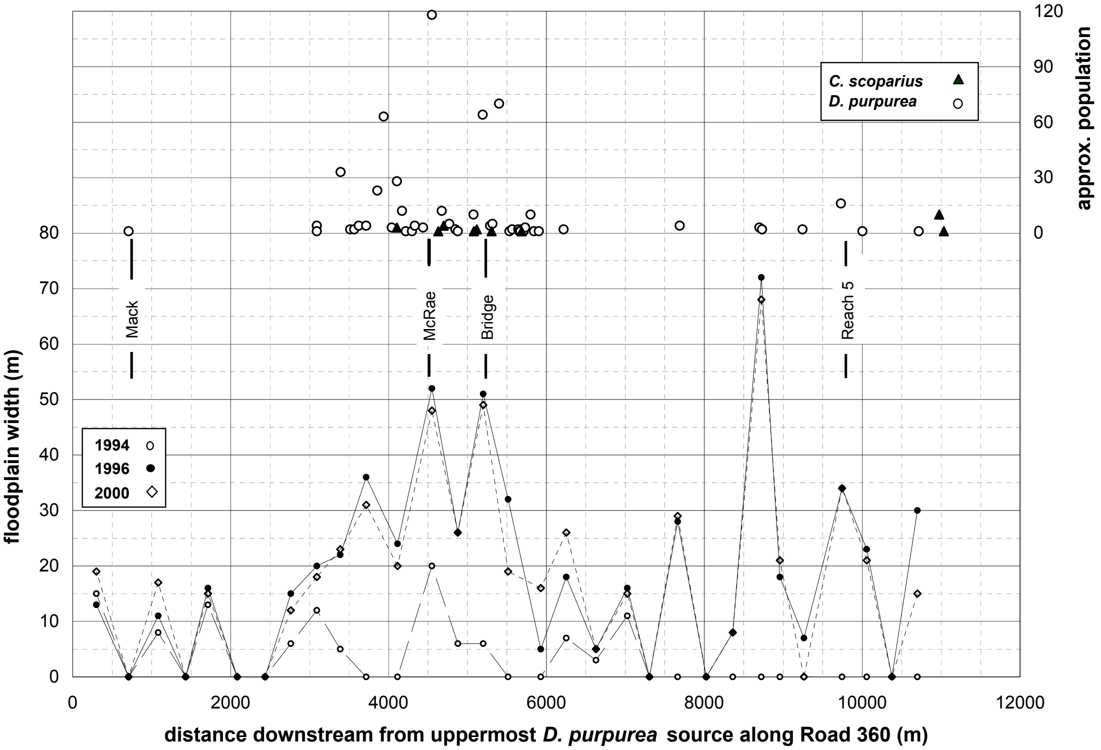

Figure 22. Unvegetated floodplain width along Lookout Creek in relation to *Cytisus scoparius* and *Digitalis purpurea* distribution along streams in 2003. Figure shows unvegetated floodplain widths measured from aerial photographs of 1994, 1996, and 2000 (primary y-axis) and approximate populations of *Cytisus scoparius* and *Digitalis purpurea* observed in streams in 2003 (secondary y-axis) with distance downstream of the uppermost *Digitalis purpurea* seed source along Road 360 shown in Figure 20.

2000 was high; all *C. scoparius* patches occurred in this reach (Figure 22). *D. purpurea* was observed upstream in narrower unvegetated sections of Lookout Creek, but was largely absent downstream of transect 16 where the 1996/2000 unvegetated floodplain narrowed. Further downstream *D. purpurea* reappeared discontinuously, but was mostly restricted to wider unvegetated stream sections (Figure 22). Vegetation removal 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* (van Baalen 1982, Tarrega *et al.* 1992, Bossard 1993, McAlpine and Drake 2002). However, *C. scoparius* or *D. purpurea* plants occupied only small fractions of the total exposed, and apparently suitable, floodplain surface, and within patches individual plant locations were not related to light levels.

Experimental trials

Maximum germination

Tetrazolium chloride testing indicated that *C. scoparius* seeds had very high viability. On average 99% (± 1%) of the *C. scoparius* seeds were potentially viable prior to treatment. Of the 190 seeds tested, 178 (94 ± 6%) were normal, 3 (2 ± 3%) abnormal, 6 (3 ± 4%) hard, and 3 (1 ± 1%) dead (Table 6). In germination trials, the "optimal" treatment for *C. scoparius* seeds (submergence in 55 C water for 2 hours before planting on blotter paper) was unsuccessful in germinating all of the viable seeds. This treatment resulted in a lower germination rate than the seed viability; however this treatment did markedly increase germination rates over untreated samples. "Optimal" treatment achieved 74% germination compared to only 43% (± 22%) for untreated control samples. Floating and sinking seeds had similar germination rates (40 and 30% respectively) [Figure 23(a), Table 7].

The *D. purpurea* seeds used in this study had a lower viability than *C. scoparius* seeds. In viability tests, 86 (43 ± 6%) of 199 *D. purpurea* seeds were normal, 53 (27 ± 1%) were abnormal, and 60 (30 ± 12%) were dead (Table 6). In other words, less than 70% (± 10%) of the *D. purpurea* seeds were viable. In germination trials conducted with *D. purpurea*,

Table 6. *Cytisus scoparius* and *Digitalis purpurea* seed viability

Species	Sample size	Normal *(%)*	Abnormal *(%)*	Hard *(%)*	Dead *(%)*	Potentially viable *(%)*
C. scoparius	95	91	3	5	1	99
	95	97	0	1	2	98
	Average	***94***	***2***	***3***	***1***	***99***
D. purpurea	102	39	25	---	35	65
	97	47	28	---	25	75
	Average	***43***	***27***	***---***	***30***	***70***

control groups receiving no treatment (also considered "optimal" treatment) had an average germination rate of 73% (± 4%) [Figure 23(b), Table 7].

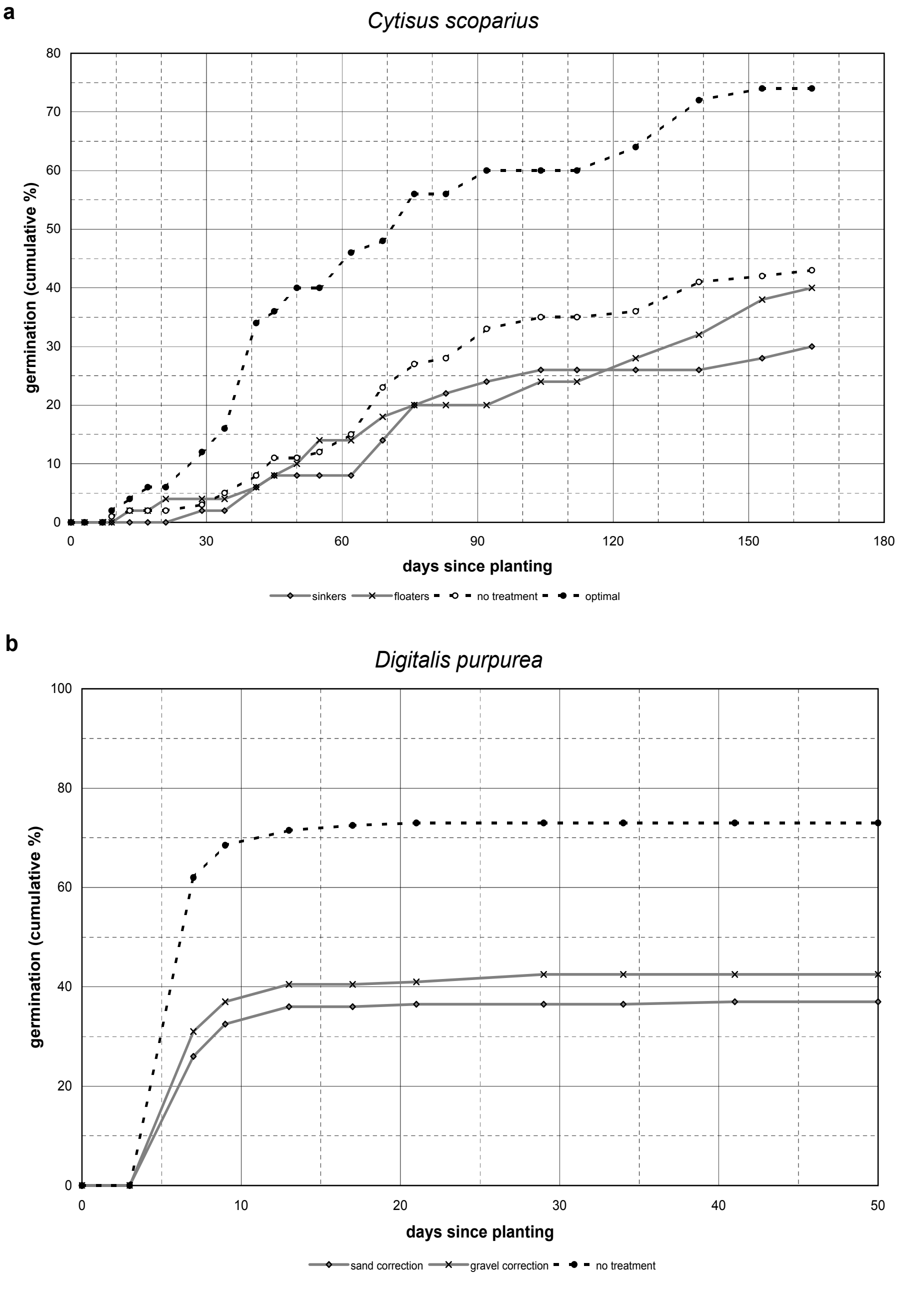

Figure 23. Baseline germination of *Cytisus scoparius* and *Digitalis purpurea* seeds. (a) Germination rates for untreated (sinkers, floaters, no treatment) and "optimally" treated (warm water soak) *Cytisus scoparius* seeds. (b) Germination rates for untreated (also considered "optimally" treated) *Digitalis purpurea* seeds. Sand correction and gravel correction germination rates represent germination of seeds retrieved from gravel and sand scarification mixtures without tumbling. These values were used to adjust germination rates of scarification treatments.

Table 7. Results of *Cytisus scoparius* scarification trials

Treatment type	Tumbling details		Scarification mixture composition			**Germination**	**Change from control**
	rotations	*duration (min)*	*mixture type*	*sediment (%)*	*water (%)*	***(%)***	
control	---	---	---	---	---	**54**	**---**
control	---	---	---	---	---	**32**	**---**
					Average (error)	**43 (± 22)**	**---**
optimal	---	---	---	---	---	**74**	**31**
floats	---	---	---	---	---	**40**	**-3**
sinks	---	---	---	---	---	**30**	**-13**
tumbled	100	2	very coarse sand	50	50	**28**	**-15**
tumbled	500	10	very coarse sand	50	50	**28**	**-15**
tumbled	1000	20	very coarse sand	50	50	**28**	**-15**
tumbled	2000	40	very coarse sand	50	50	**18**	**-25**
tumbled	100	2	fine gravel	50	50	**16**	**-27**
tumbled	500	10	fine gravel	50	50	**40**	**-3**
tumbled	1000	20	fine gravel	50	50	**42**	**-1**
tumbled	2000	40	fine gravel	50	50	**38**	**-5**
tumbled	100	2	v.c. sand/f. gravel mix	100	0	**50**	**7**
tumbled	100	2	v.c. sand/f. gravel mix	75	25	**62**	**19**
tumbled	100	2	v.c. sand/f. gravel mix	50	50	**50**	**7**
tumbled	100	2	v.c. sand/f. gravel mix	25	75	**32**	**-11**
tumbled	100	2	v.c. sand/f. gravel mix	0	100	**30**	**-13**
tumbled	1000	20	v.c. sand/f. gravel mix	100	0	**30**	**-13**
tumbled	1000	20	v.c. sand/f. gravel mix	75	25	**40**	**-3**
tumbled	1000	20	v.c. sand/f. gravel mix	50	50	**38**	**-5**
tumbled	1000	20	v.c. sand/f. gravel mix	25	75	**36**	**-7**
tumbled	1000	20	v.c. sand/f. gravel mix	0	100	**42**	**-1**

Germination conditions: moist blotter papers, 8 hrs per day artificial light, temperature 20 C

Determining the reference point

Germination trials were also performed to establish a correction for seed losses incurred during the seed retrieval process after tumbling (details of seed loss correction trials in Methods). Seed loss correction trials had germination rates averaging 37% (± 6%) for recovery from very coarse sand and 42.5% (± 3%) for recovery from fine gravel [Figure 23(b), Table 8]. The germination rate for untreated seeds was 73%. Therefore, a correction factor (multiplier) of 1.97 (73% divided by 37%) was used to adjust germination rates for tumbling treatments conducted in very coarse sand, and a correction factor of 1.72 (73% divided by 42.5%) was used to adjust germination rates for tumbling treatments conducted in fine gravel. An intermediate correction factor (1.84) was used to adjust germination rates for tumbling treatments in a mixture of very coarse sand and fine gravel. Results of the germination trials discussed below

Table 8. Results of *Digitalis purpurea* scarification trials

Treatment type	Tumbling details		Scarification mixture composition			**Observed**	Correction	**Adjusted**	**Change from**
	rotations	*duration (min)*	*mixture type*	*sediment (%)*	*water (%)*	**germination *(%)***	factor*	**germination *(%)****	**control**
control	---	---	---	---	---	**71**	---	**---**	**---**
control	---	---	---	---	---	**75**	---	**---**	**---**
					Average (error)	**73 (± 4)**	---	**---**	**---**
correction	1	---	very coarse sand	50	50	**34**	---	**---**	**-39**
correction	1	---	very coarse sand	50	50	**40**	---	**---**	**-33**
					Average (error)	**37 (± 6)**	---	**---**	**-36**
correction	1	---	fine gravel	50	50	**44**	---	**---**	**-29**
correction	1	---	fine gravel	50	50	**41**	---	**---**	**-32**
					Average (error)	**42.5 (± 3)**	---	**---**	**-31**
tumbled	100	2	very coarse sand	50	50	**30**	1.97	**59**	**-14**
tumbled	500	10	very coarse sand	50	50	**12**	1.97	**24**	**-49**
tumbled	1000	20	very coarse sand	50	50	**32**	1.97	**63**	**-10**
tumbled	2000	40	very coarse sand	50	50	**29**	1.97	**57**	**-16**
tumbled	100	2	fine gravel	50	50	**12**	1.72	**21**	**-52**
tumbled	500	10	fine gravel	50	50	**15**	1.72	**26**	**-47**
tumbled	1000	20	fine gravel	50	50	**1**	1.72	**2**	**-71**
tumbled	2000	40	fine gravel	50	50	**0**	1.72	**0**	**-73**
tumbled	100	2	v.c. sand/f. gravel mix	100	0	**30**	1.84	**55**	**-18**
tumbled	100	2	v.c. sand/f. gravel mix	75	25	**28**	1.84	**51**	**-22**
tumbled	100	2	v.c. sand/f. gravel mix	50	50	**19**	1.84	**35**	**-38**
tumbled	100	2	v.c. sand/f. gravel mix	25	75	**20**	1.84	**37**	**-36**
tumbled	100	2	v.c. sand/f. gravel mix	0	100	**63**	**---**	**---**	**-10**
tumbled	1000	20	v.c. sand/f. gravel mix	100	0	**21**	1.84	**39**	**-34**
tumbled	1000	20	v.c. sand/f. gravel mix	75	25	**7**	1.84	**13**	**-60**
tumbled	1000	20	v.c. sand/f. gravel mix	50	50	**5**	1.84	**9**	**-64**
tumbled	1000	20	v.c. sand/f. gravel mix	25	75	**17**	1.84	**31**	**-42**
tumbled	1000	20	v.c. sand/f. gravel mix	0	100	**81**	**---**	**---**	**8**

*Adjusted germination rates corrected for seed loss incurred during seed recovery after tumbling treatments. Correction factor equals average germination rate of control samples (73%) divided by germination rate for the relevant correction trial (37% for v.c. sand, 42.5% for fine gravel, 39.75% for v. c. sand/fine gravel mixtures).

Germination conditions: moist blotter papers, 8 hrs per day artificial light, temperature 20 C

are presented as adjusted germination rates to normalize germination results and facilitate identification of treatments effects.

Effect of scarification on germination

C. scoparius germination was reduced by increased abrasion (i.e., increased amount of tumbling). *C. scoparius* germination rates were negatively related to abrasion in scarification mixtures of very coarse sand and very coarse sand with fine gravel. Germination was only 18% for seeds tumbled 2000 times in very coarse sand compared to 28% for seeds tumbled 100, 500, and 1000 times [Figure 24(a), Table 7]. Additionally, germination rates were generally higher (50, 62, and 50%) for seeds tumbled 100 rotations than seeds tumbled for 1000 rotations (30, 40, and 38%) in mixtures of ratios of 1:0, 3:1, and 1:1 very coarse sand and fine gravel to

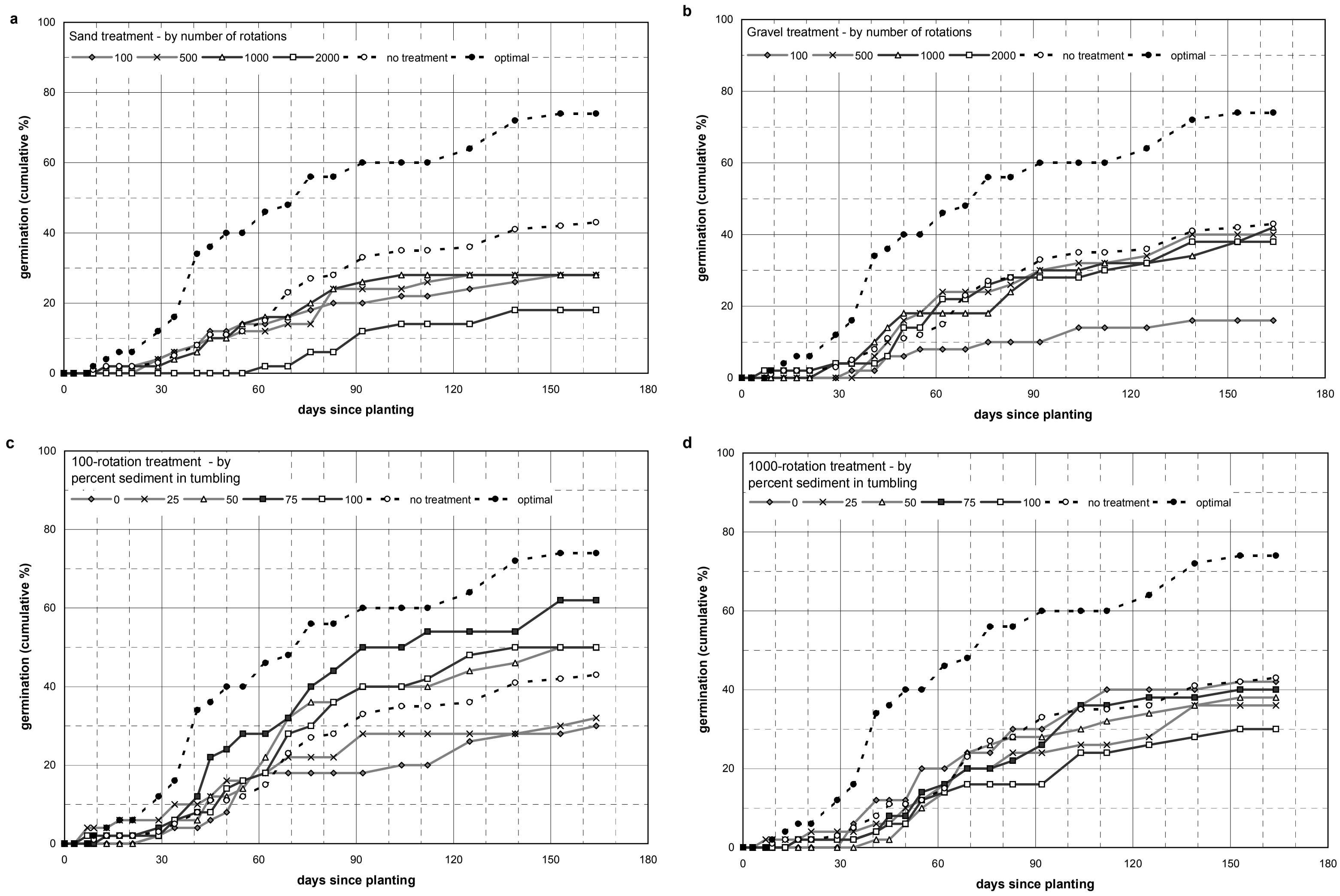

Figure 24. Germination of *Cytisus scoparius* seeds after scarification treatments in sediment and water. (a) Germination after tumbling in very coarse sand and water. (b) Germination after tumbling in fine gravel and water. (c) Germination after 100 rotations in mixtures of sediment and water. (d) Germination after 1000 rotations in mixtures of sediment and water.

water, respectively [Figures 24(c) and (d), Table 7]. However, seeds tumbled in fine gravel for 100 rotations had lower germination rates (16%) than seeds tumbled for 500, 1000, and 2000 rotations, which had germination rates of 40, 42, and 38% [Figure 24(b), Table 7]. Of the 18 *C. scoparius* seed samples receiving scarification treatments, 15 had reduced germination rates compared to the average for untreated seeds.

D. purpurea germination was negatively related to scarification in tumbling treatments with very coarse sand and fine gravel. Adjusted germination rates for *D. purpurea* after tumbling with very coarse sand and water were 59, 24, 63, and 57% for treatments of 100, 500, 1000, and 2000 rotations [Figure 25(a), Table 8]. Although germination rates were not related to the amount of abrasion in very coarse sand, germination rates of seeds scarified by very coarse sand on average were 22% below the average germination rate for untreated seeds (73%). When tumbled, adjusted germination rates of *D. purpurea* were negatively related to abrasion with fine gravel; rates were 21 and 26% after tumbling for 100 and 500 rotations and 2 and 0% after 1000 and 2000 rotations [Figure 25(b), Table 8]. Germination rates are of *D. purpurea* after scarification with fine gravel on average were 61% below the average germination rate for untreated seeds (73%). Germination rates of *D. purpurea* seeds also were negatively related to increased tumbling in mixture ratios of 1:0, 3:1, 1:1, and 1:3 of very coarse sand and fine gravel to water (55, 51, 35, and 37% for 100 rotations versus 39, 13, 9, and 31% for 1000 rotations, respectively) [Figures 25(c) and (d), Table 8]. These germination rates of *D. purpurea* seeds in sediment and water mixtures on average were 29 percentage points lower than germination rates for untreated seeds (73%) after tumbling for 100 rotations and 50 percentage points lower after tumbling for 1000 rotations.

Effect of sediment to water proportion in scarification mixture on germination

C. scoparius germination was not clearly related to the proportion of sediment versus water in the scarification mixtures. *C. scoparius* seed germination was weakly positively related to

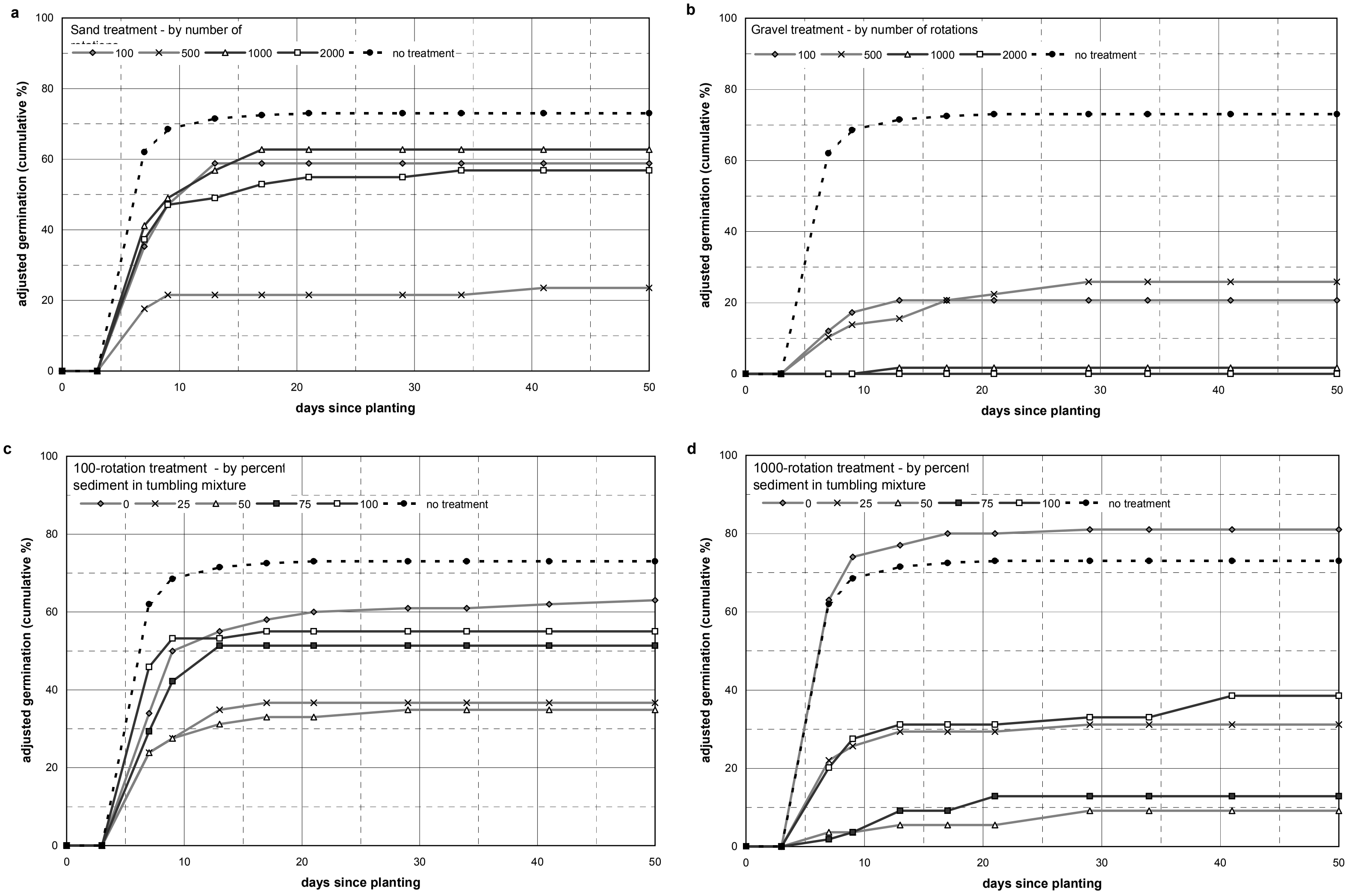

Figure 25. Germination of *Digitalis purpurea* seeds after scarification treatments in sediment and water. (a) Germination after tumbling in very coarse sand and water. (b) Germination after tumbling in fine gravel and water. (c) Germination after 100 rotations in mixtures of sediment and water. (d) Germination after 1000 rotations in mixtures of sediment and water.

the proportion sediment in the scarification mixture for tumbling treatments of 100 rotations. Seeds tumbled 100 times had germination rates of 50, 62, 50, 32, and 30% as sediment to water ratios decreased from 1:0, 3:1, 1:1, 1:3, to 0:1. The 3 highest germination rates here averaged 54% for tumbling treatments in sediment to water ratios of 1:0, 3:1, and 1:1, slightly above the control group germination rate of 43% [Figure 24(c), Table 7]. At 1000 rotations, no clear relationship exists between the proportion sediment and germination of *C. scoparius*. Seeds tumbled 1000 times had germination rates of 30, 40, 38, 36, and 42% for mixtures of 1:0, 3:1, 1: 1, 1:3, and 0:1 sediment to water, respectively [Figure 24(d), Table 7]. These rates are generally similar to the average germination for the control group. Together, the results of scarification trials in mixtures of different sediment to water proportions may suggest some reduction of *C. scoparius* germination in seeds in response to increasing water content in the scarification mixture, but only when abrasion time is short.

D. purpurea germination was inversely related to water content in the scarification mixture and the length of tumbling in scarification mixtures, especially when the proportion of sediment was roughly equal to the proportion of water. Adjusted germination rates of *D. purpurea* were 55, 51, 35, and 37% after 100 rotations in mixtures of 1:0, 3:1, 1:1, and 1:3 proportions of sediment to water, compared to 63% after 100 rotations in water [Figure 25(c), Table 8]. After 1000 rotations, adjusted germination rates were not related to sediment proportion in the scarification mixture. Adjusted germination rates of *D. purpurea* were 39, 13, 9, and 31% after 1000 rotations in mixtures of ratios 1:0, 3:1, 1:1, and 1:3 of sediment to water, compared to 81% after 1000 rotations in water [Figure 25(d), Table 8]. These results indicate that the proportion of sediment in the scarification mixture is important and suggest that a combination of scarification and soaking together may have the greatest negative effect on seed germination.

Effect of scarification mixture particle size on germination

Germination of *C. scoparius* was not consistently related to the texture (i.e., coarseness) of the scarification mixture used in tumbling treatments. Germination rates of *C. scoparius* were 28, 50, and 16% after 100 rotations in 1:1 sediment to water mixtures of very coarse sand, very coarse sand with fine gravel, and fine gravel, respectively, compared to 28, 42, and 38% after 1000 rotations [Figures 24(a) to (d), Table 7].

Germination of *D. purpurea* was negatively related to the coarseness of the scarification mixture. Adjusted germination rates of *D. purpurea* were 59% in very coarse sand, 35% in very coarse sand and fine gravel, and 21% in fine gravel, after 100 rotations in 1:1 sediment to water mixtures and 63% in very coarse sand, 9% in very coarse sand and fine gravel, and 2% in fine gravel after 1000 rotations in 1:1 sediment to water mixtures [Figures 25(a) to (d), Table 8].

Effect of substrate on germination

Germination rates of *C. scoparius* were high in all but the extremely coarse and fine substrate types. Germination rates ranged from 80 to 90% in substrates of medium sand, coarse

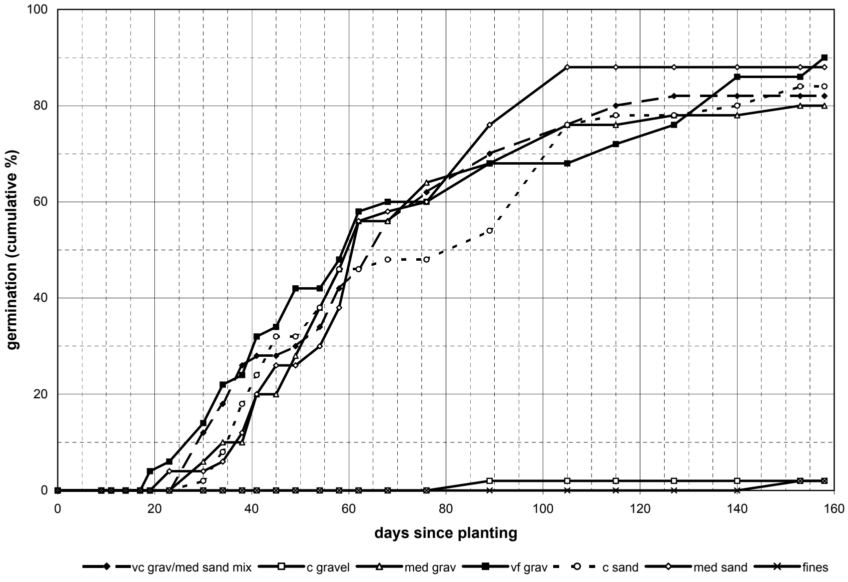

Figure 26. Germination of *Cytisus scoparius* seeds in different substrates. Substrates included very coarse gravel and medium sand mix, coarse gravel, medium gravel, very fine gravel, coarse sand, medium sand, and fines.

Table 9. Results of *Cytisus scoparius* and *Digitalis purpurea* substrate trials

Substrate type	Sediment composition		**Germination percent**	
	particle type	*% by volume*	***C. scoparius***	***D. purpurea***
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		

Germination conditons: 10 to 14 hrs per day indirect natural light, temperatures 15 to 24 C

sand, very fine gravel, medium gravel, and a very coarse sand and medium gravel mixture (Figure 26, Table 9). These germination rates exceed the germination rate for the control sample (which also was "optimally" treated) that was planted on blotter paper as part of the scarification trials discussed earlier (Figure 23, Table 7). Seeds planted in both the coarsest (coarse gravel) and finest substrates (fines, consisting of fine sand, very fine sand, silt, and clay) had very low germination (2%) (Figure 26, Table 9).

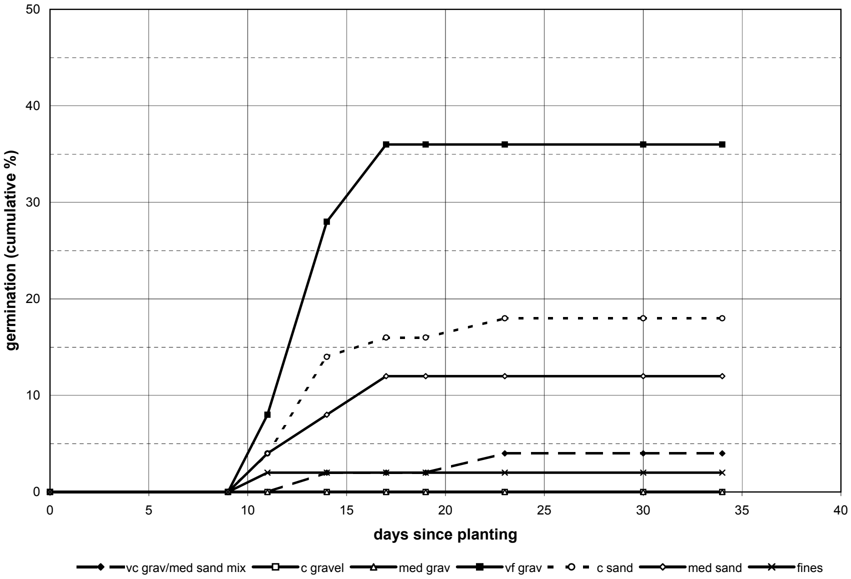

Figure 27. Germination of *Digitalis purpurea* seeds in different substrates. Substrates included very coarse gravel and medium sand mix, coarse gravel, medium gravel, very fine gravel, coarse sand, medium sand, and fines.

Germination rates of *D. purpurea* were highest in moderately coarse substrates. Germination was highest for *D. purpurea* seeds planted in very fine gravel (36%) and decreased with substrate fining and coarsening. Coarse sand (18%) and medium sand (12%) had the next highest germination rates. Coarser substrates such as medium gravel (0%), coarse gravel (0%), and a mixture of very coarse gravel and medium sand (4%) all had consistently low germination rates, as did seeds planted in fines (2%) (Figure 27, Table 9).

Floating ability

In flotation trials, less than 10% of *C. scoparius* seeds floated when placed in water and no seeds floated for more than 36 hours. On average, floating time for *C. scoparius* seeds was approximately 2 hours. In contrast, 100% of *D. purpurea* seeds floated when placed in water; over 80% were still floating after 12 hours and some seeds floated for more than 48 hours. The average floating time for *D. purpurea* seeds was approximately 22 hours [Figure 28(a)]. Additionally, nearly half (49%) of the *D. purpurea* seeds germinated subsequent to sinking and while immersed in water. Of the *D. purpurea* seeds that germinated, the average elapsed time from the start of the flotation trial to germination was 10.2 days. *D. purpurea* seedlings were also observed floating on the water surface after 10 days. By the end of the flotation trials after 17 days, 22% of the seeds had germinated and were floating [Figure 28 (b)]. One *C. scoparius* seed also germinated after 22 days of immersion in water, after the flotation trials had been terminated.

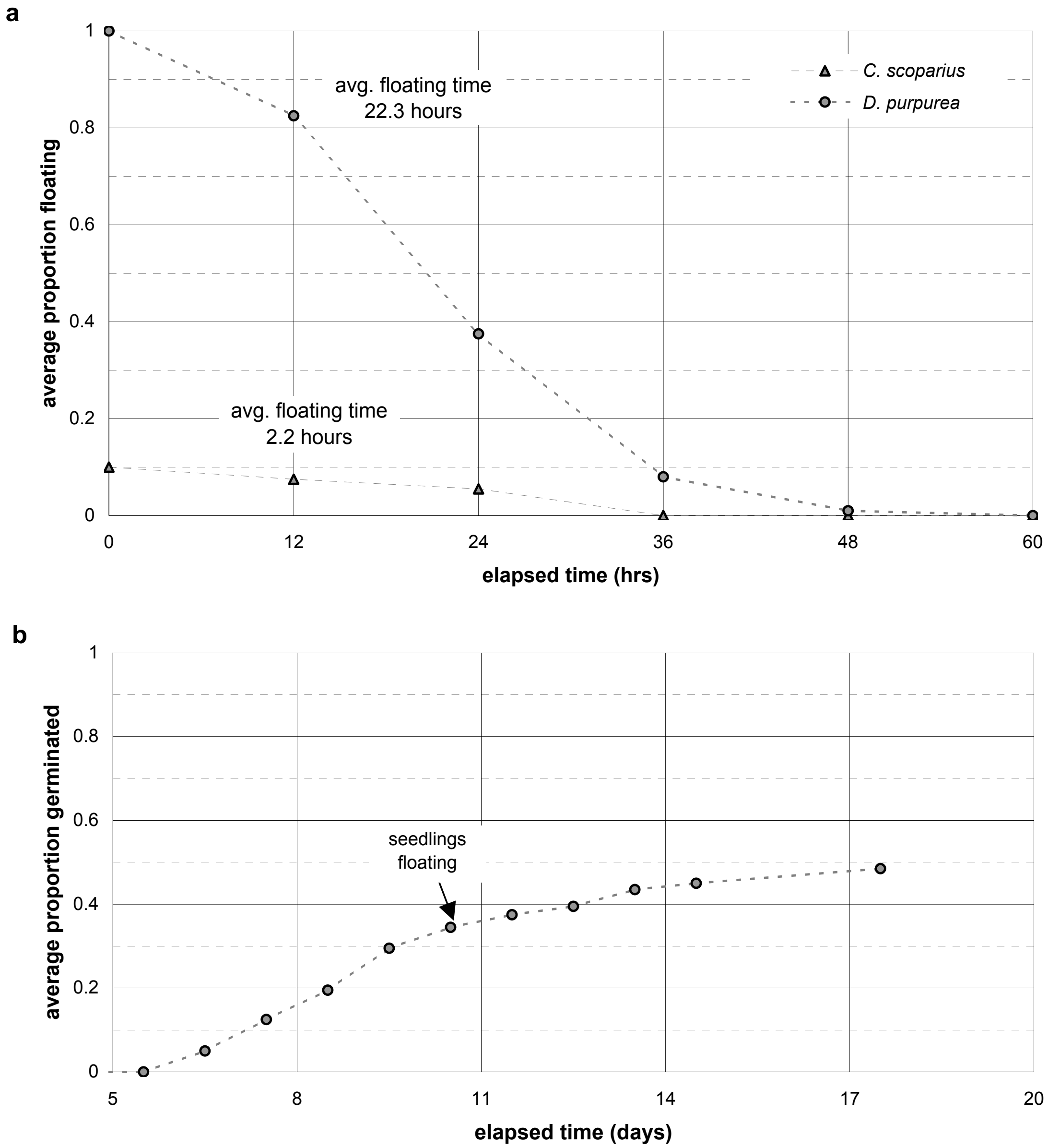

Figure 28. Floating ability and germination of *Cytisus scoparius* and *Digitalis purpurea* seeds in water. (a) Seed floating duration. (b) Seed germination while immersed in water.

DISCUSSION

Successful plant invasion of a stream network requires 1) a source plant population from which propagules can be derived; 2) a transport mechanism to get viable seeds into the stream network; and 3) stream sinks with suitable site conditions for seed deposition and germination and seedling establishment. Limitation by sources, transport mechanisms, or sinks will prevent species from invading the stream network.

Hypothesis 1: Source limitation

The results of this study support the hypothesis that the invasion of *C. scoparius* and *D. purpurea* in streams is limited by the locations of seed sources present on the hillslopes along roads and in clear-cut patches. The distribution of *C. scoparius* and *D. purpurea* in the Andrews is consistent with downgradient movement of seeds from hillslopes into streams. In 2003, all *C. scoparius* and *D. purpurea* stream patches occurred downgradient of potential hillslope seed sources where *C. scoparius* or *D. purpurea* occurred in 1994, 2002, or 2003 (Figures 9 to 12).

C. scoparius occurred throughout the Andrews on hillslopes, but *C. scoparius* patches in streams were mainly limited to the middle reaches of McRae and Lookout creeks where it was also present nearby along upgradient roads and in clear-cuts (Figures 9 and 10). The spatial extent (i.e., uppermost occurrences) of *D. purpurea* in the Andrews streams was similar to its extent on the hillslopes. *D. purpurea* occurred most frequently and abundantly in the middle reaches of Lookout Creek; however, patches also occurred upstream in McRae and Lookout creeks at stream sites located downgradient from the uppermost hillslope sources (Figures 11 and 12). On hillslopes *D. purpurea* was only present at low elevations in 2003 and was noticeably uncommon along roads on the north side of Lookout Creek (roads 1508 and 320 and upper Road 1506). Any apparent elevation cutoff in the distribution of *D. purpurea* is likely a reflection of its abundance on hillslopes along Road 360, a low-elevation road that parallels Lookout Creek, where it likely first became abundant in this landscape. The general absence of *D. purpurea* along low-elevation roads on the north side of Lookout Creek, is probably because seeds are less likely to be dispersed by local wind processes or by vehicles from major seed sources along Road 360 to these more distal parts of the road network. The strong similarity between spatial extent of *D. purpurea* on hillslopes and in streams is most likely because of limitation by upgradient hillslope source locations.

Research has shown elevational limitations on the distribution of some exotic species along roads, but without decoupling it from climatic factors (Forcella and Harvey 1983, Parendes 1997, Pauchard and Alaback 2004). In a controlled experiment, *D. purpurea* seed germination was greatest at temperatures between 20 and 35 C, but was impaired at temperatures of 16 C (approximately 80% of maximum germination) and 12 C (37% of maximum germination); few seeds germinated below a temperature of 12 C (van Baalen 1982). In its native range, *D. purpurea* seedling survival decreased with altitude, but was not correlated with minimum temperatures between –4 C and –9 C; plant growth was negatively related to altitude, but mature plants incurred damage only at temperatures below –12 C (Bruelheide and Heinemeyer 2002). *Wilson et al.* (1992) found that *D. purpurea* distribution in New Zealand occurred along gradients of precipitation (where annual precipitation exceeded 1500 mm and where number of rain days exceeded 100), but found little relationship to temperature, light, frost days, and water deficit.

In the Andrews, mean monthly minimum temperatures are between –1 C and –2 C in the winter and exhibit only a minimal gradient with elevation. Cooler spring and fall temperatures at higher elevations (Figure 3) during periods of *D. purpurea* seed germination may decrease seedling recruitment, but are unlikely to exclude plants from these parts of the landscape. Annual precipitation ranges from 2300 mm to 3500 mm in the Andrews and occurs mostly during winter months. Precipitation amount is unlikely to limit the distribution of *D. purpurea* in this study, but timing of precipitation and summer drought may affect plant survival (Bruelheide and Heinemeyer 2002). Still, while climatic factors may decrease

D. purpurea survival at higher elevations, the complete absence of *D. purpurea* from higher-elevation hillslopes, and therefore from higher elevations in streams, was most likely because of a general lack of seed dispersal to these areas.

Hypothesis 2: Transport limitation

Debris flows and flood flows appear to be viable mechanisms for transporting *C. scoparius* and *D. purpurea* seeds from hillslope sources into mainstem streams as well as for dispersing seeds within the stream network. Furthermore, the spatial and temporal distributional patterns of *C. scoparius* and *D. purpurea* found in this study support the hypothesis that seeds are moving downgradient from hillslope sources into streams and that key transport events are important in facilitating the invasion of streams. *C. scoparius* and *D. purpurea* were present on hillslopes in the Andrews, occurring along roads and in clear-cuts as early as the 1970s (Franklin and Dyrness 1971; J. Franklin, personal communication); however, neither species was reported in streams until 2002 (Parendes 1997; Parendes and Jones 2000; Ashley *et al.* unpublished; J. Jones, personal communication). In 2003, at their upstream extent in Lookout and McRae creeks, *C. scoparius* and *D. purpurea* patches were most often in stream reaches away from the road and in the vicinity of tributary channels where debris flows occurred in 1996 and where seed sources were also present on hillslopes. Circumstantial evidence suggests that *C. scoparius* and *D. purpurea* seeds were probably transported from hillslopes source into valley bottoms and mainstem stream reaches in 1996 by floodwaters and debris flows. Furthermore, low-order stream channels that were scoured by debris flows in 1996 would likely be more effective conduits for seed movement from hillslopes into streams during subsequent years.

Experimental scarification and flotation trials show that *C. scoparius* and *D. purpurea* seeds may be capable of surviving dispersal by debris flows and flood waters, especially when the texture of the moving sediment is fine (Figures 24 and 25). Additionally, *D. purpurea* seeds are capable of floating (Figure 28) and consequently may ride higher in the water or sediment column during transport, enabling them to avoid more intense abrasion that may occur when particles are transported near the bottom of a debris flow or along the streambed. In a study of revegetation on debris flow paths, *Gecy* (1988) found that seedling establishment from the residual seed bank was responsible for most of the revegetation of fine and gravel debris flow deposits, whereas vegetative regrowth was more effective on scoured surfaces. This supports the idea that seeds can survive transport in debris flows.

C. scoparius have large and heavy seeds which require powerful external dispersal mechanisms for long-distance transport, but wind may be capable of transporting small and light *D. purpurea* seeds into streams from roads when they are near. However, the steep, forested terrain in the Andrews may limit the effectiveness of wind as a long-distance dispersal mechanism for connecting *D. purpurea* hillslope seed sources to streams. Prevailing winds in the Andrews blow generally from the southwest in an upstream direction between mid-December and mid-October with peak wind speeds occurring during the months from May to August; winds tend to blow from the northeast in a downstream direction between mid-October and mid-December (McKee 2003). This means that wind may transport seeds upstream from hillslope sources or in-stream sources during the late summer and early fall months after they have been dispersed from the plant. However, finer temporal- and spatial-scale observations of summer wind flow in steep tributary catchments suggest that near the ground surface downgradient air movement dominates, occurring on average more than 75% of the time (Pypker unpublished data).

Dispersal distances for *D. purpurea* seeds by passive autochory (self dispersal) are believed to be approximately 4 m (Hanson 2000) and exceed 5.5 m with increasing wind velocity and dispersal height (Bruelheide and Heinemeyer 2002). However, wind dispersal is less effective on coarse surfaces, especially when seed size and mass are small (Chambers *et al.* 1991, Johnson and Fryer 1992); therefore, large bed particles in the Andrews stream network, which have a mean diameter between 10 and 15 cm (Swanson 2002), probably also limit long-distance wind dispersal of *D. purpurea* within and along stream corridors. Most importantly, the general absence of *D. purpurea* from the road network in areas where it occurred in the stream and where the road is near the stream, is evidence that wind is probably not a primary mechanism for long-distance dispersal of *D. purpurea* seeds in this landscape. It is unlikely that upstream *C. scoparius* and *D. purpurea* patches were derived from wind-dispersed seeds.

Hypothesis 3: Sink limitation

The results of this study strongly support the hypothesis that *C. scoparius* and *D. purpurea* patches in streams are limited by the availability of sinks, sites with suitable environmental conditions for the deposition of seeds as well as the eventual germination of seeds and establishment and persistence of seedlings. In 2003, *C. scoparius* and *D. purpurea* patches occurred most frequently in unconstrained, low-gradient stream reaches (Figures 20 and 21) where the unvegetated floodplain was wide and light levels were high in 1996 and 2000 (Figure 22). Additionally, *C. scoparius* and *D. purpurea* patches generally occurred at sites protected from flood scour by local floodplain features (Figures 13 to 19) where seeds were more likely to be deposited and seedlings able to persist. Stream patches were not clearly related to substrate texture or moisture levels in this study; furthermore, no clear relationship with light levels was observed at the within-patch scale. Reach-scale fluvial geomorphic features and processes such as large wood deposits, secondary channels, and channel migrations and bank overtopping flows, may promote seed deposition and enable the establishment and persistence of *C. scoparius* and *D. purpurea* in streams (Figure 29). *C. scoparius* and *D. purpurea* patches occurred only at locations where seeds were deposited and germinated, and where seedlings were allowed to establish; however, it is not clear what factors were most limiting.

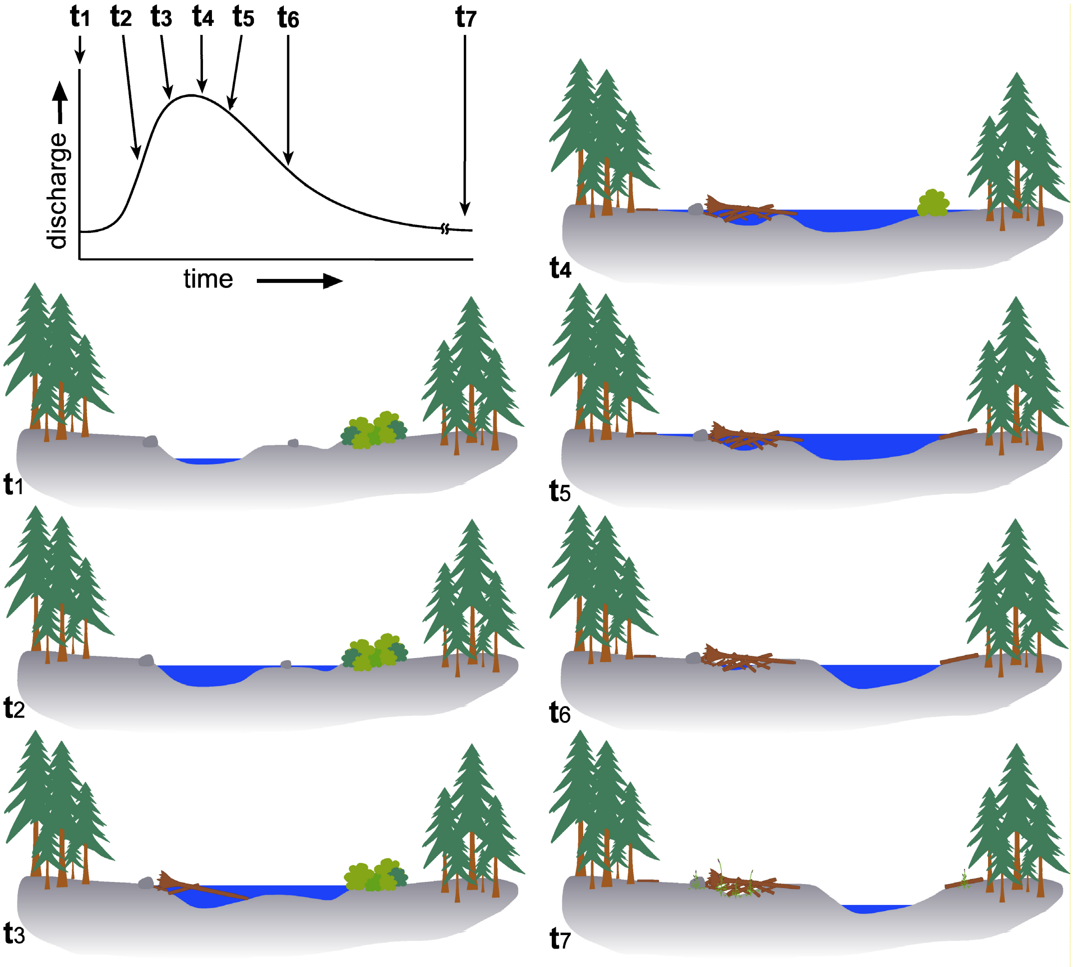

Figure 29. Schematic illustration of fluvial geomorphic features and flooding processes that promote seed deposition and enable the establishment of invasive plants in streams. t1: at low flow prior to flood event. t2: on rising limb of hydrograph, flow overtopping banks and inundating secondary channel. t3: discharge nearing peak with wood accumulating in primary channel and some scouring of secondary channel. t4 and t5: at peak discharge with more wood accumulating in what was the primary channel, diverting primary flow into what was the secondary channel. Floodplain vegetation is being scoured and some large wood depositing at floodplain margins. t6: on falling limb of hydrograph with flow abandoning channel where debris jam occurred. t7: at low flow, invasive species germinating and establishing in protected areas in abandoned channel and downstream of floodplain obstructions.

Seed deposition

Hydrologic principles (Manning's equation for $V=R^{2/3}S^{1/2}/n$, where V is velocity, R is hydraulic radius, S is slope, n is boundary roughness) state that flow velocity is proportional to slope, so low-gradient reaches have relatively low velocities compared to other parts of the stream network. As flow velocities decrease in low-gradient reaches the cross-sectional area expands in order to maintain stream discharge (Q = VA, where Q is discharge, V is velocity, A is cross-sectional area). This means that in addition to dropping in velocity, flows in low-gradient reaches will cover more floodplain surface area. Accordingly, invasive species seed deposition within the stream network should be high in low-gradient stream reaches where flows are slower and cover a larger depositional surface area.

Seed deposition has been closely tied to sediment deposition processes in fluvial systems (Schneider and Sharitz 1988, Goodson *et al.* 2003). Seed deposition was most common in low-velocity environments such as eddies and flow expansions in an artificial flume study (Merritt and Wohl 2002) and wooden cubes used as seed mimics deposited in low-velocity areas in a natural river (Nilsson *et al.* 1991). Also, seeds are often trapped by emergent objects and at floodplain margins (Schneider and Sharitz 1988, Skoglund 1990, Johansson and Nilsson 1993). Depositional and lateral channel movement processes dominate in unconstrained reaches of Lookout Creek where the gradient tends to be lower (Grant and Swanson 1995). Large wood exerts strong controls on channel morphology and sediment transport dynamics in streams at the Andrews by forcing channel avulsions and creating sites for sediment deposition (Keller and Swanson 1979, Nakamura and Swanson 1993, Faustini 2000, Faustini and Jones 2002). In 1996, large volumes of wood deposited along streams (Czarnomski 2003, Dreher unpublished data) and flows expanded into secondary channels in low-gradient reaches; in some places channels avulsed, abandoning their pre-1996 course. Obstructions on the floodplain and elevated bars and terraces provide additional protection from scour of overbank flows and likely promote seed deposition (Figures 13 to 17). In higher-gradient reaches, large wood deposits may slow flows by pooling water upstream of obstructions or in protected areas immediately downstream, allowing seeds to deposit locally in these higher-energy stream reaches.

Seed germination and seedling establishment

Stream corridors in the Andrews were narrow and floodplain surfaces were densely vegetated prior to 1996 (Figure 22). Geomorphic processes acting along McRae and Lookout creeks in 1996 removed vegetation, exposing large areas of the floodplain surface (Johnson *et al.* 2000). The widening of the stream corridor provided elevated light levels in large portions of the stream network where light levels were probably limiting prior to 1996, allowing deposited seeds to germinate and become established. Lateral channel migrations isolated parts of the active floodplain from the main channel through 2003 and probably enabled *C. scoparius* and *D. purpurea* seedlings to persist at sites. Local features like logs, stumps, large wood jams, boulders, or standing vegetation also create local slope breaks and may have protected established *C. scoparius* and *D. purpurea* patches from scouring floods in 1997, 1999, and 2000. (Figures 13 to 19).

Locations of *C. scoparius* and *D. purpurea* stream patches in this study were apparently not a result of differential seed germination rates in substrate textures and also did not appear to be related to moisture levels at or near the ground surface. Other studies have found higher *C. scoparius* seed germination rates in fine substrate (Williams 1981); however, this finding was not fully supported by germination trials in this study (Figure 26, Table 9). *D. purpurea* patches in streams were not substrate-specific, but in germination trials *D. purpurea* seeds exhibited greater sensitivity to substrate texture. The tendency for *C. scoparius* to occur in fine substrate (Figure 18) and the tendency for *D. purpurea* to occur most often amongst larger particles (Figure 18) in this study may be due to greater seed deposition and scour protection that promote seedling recruitment at these sites. Water or local wind dispersal within patches may tend to disperse *D. purpurea* seeds into niches and depressions among larger particles (Reichman 1984); however, native seedling recruitment and exotic plant invasions have also been linked to other environmental site factors including water table depth (McBride and Strahan 1984, Mahoney and Rood 1992, Taylor *et al.* 1999) and soil chemical composition

(Greenberg *et al.* 1997, Gelbard and Harrison 2003) or organic content, which were not examined in this study.

Stream geomorphology and hyporheic exchange are closely linked in streams (Wondzell and Swanson 1999). This ground-surface water exchange process may increase local subsurface soil moisture levels, particularly in surface depressions or in secondary and abandoned channels where substrates may be coarser, and consequently more suitable for subsurface hyporheic flow. As a result, the water table may be higher in or near these stream features where *C. scoparius* and *D. purpurea* commonly occurred in this study. Seedling recruitment along waterways has been tied to the flood regime, with most recruitment occurring in secondary and abandoned channels or other areas where floods create suitable establishment sites by scouring vegetation and depositing fresh sediment (Auble and Scott 1998, Taylor *et al.* 1999, Cooper *et al.* 2003). Species with short reproductive cycles can persist at low floodplain elevations where inundation is frequent (Harris 1987) and during periods of infrequent flooding woody species may also become established on lower-elevation stream features (Cooper *et al.* 2003). However, maximum seedling recruitment tends to occur in areas of the floodplain where flood frequency and intensity are intermediate and where seeds and sediment can deposit, but where flows are also less likely to scour intensely (Harris 1987, Auble and Scott 1998, Rood *et al.* 1998, Taylor *et al.* 1999, Hood and Naiman 2000). On occasion, plants protected by stream features from the direct force of flow and some mature woody plants have been able to survive in areas below the high water level (McBride and Strahan 1984, Cooper 2003), where plants otherwise would be scoured by powerful flows.

Species distributions: *Cytisus scoparius* versus *Digitalis purpurea*

The distributions of *C. scoparius* and *D. purpurea* in the Andrews stream network differed greatly in 2003. Distribution patterns may be explained by interactions between their contrasting life history traits and reproductive strategies with the flood regime (Halpern 1989).

Species with long-floating seeds made up a large portion (83%) of vegetation on riverbanks in a river in northern Sweden (Johansson *et al.* 1996). *C. scoparius* patches may be more limited in streams in this study because water is less effective at transporting shorter-floating seeds (Nilsson *et al.* 1991), but seed floating ability is not necessarily the strongest indicator of dispersal distance (Danvind and Nilsson 1997). The relatively lower abundance and frequency of *C. scoparius* in most parts of the stream network and its absence from lower Lookout Creek may also reflect a biologic delay in the propagation of its invasion wave and inability to establish during the short intervals between flooding from 1996 to 2000.

C. scoparius devote resources to producing fewer large seeds, with high viability and longevity (Turner 1933 as cited in Gill and Pogge 1974, Smith and Harlen 1991, Bossard 1993); however, *C. scoparius* plants typically do not reproduce until at least their third year after germination (Gill and Pogge 1974, Smith and Harlen 1991, Bossard 1993). In contrast, *D. purpurea* plants produce large numbers of very small seeds (Salisbury 1942, Sletvold 2002) and usually reach reproductive maturity within two years of germination (van Baalen and Prins 1983, Sletvold 2002). Plants with smaller seed mass tend to have shorter juvenile periods and shorter intervals between large seed crops, and as a result are generally more effective at establishing and invading in areas with frequent disturbances (Harris 1987, Rejmanek and Richardson 1996). Additionally, *C. scoparius* reproduction can be severely limited by pollinator visitation and inability to self-pollinate (Parker 1997, Parker and Haubensak 2002). Therefore, successful invasion of the stream by *C. scoparius* may necessitate establishment of a minimum of two plants in the stream before these patches can effectively reproduce and function as seed sources.

Along the nearby McKenzie River *Planty-Tabacchi et al.* (1996) and *Tabacchi et al.* (1996) related greater species richness and greater number of exotic species in middle river reaches to the intermediate disturbance hypothesis (Connell 1978). Similar patterns were also observed along rivers in northern Sweden (Nilsson *et al.* 1989, Nilsson *et al.* 1994). In this study, *C. scoparius* and *D. purpurea* were most frequent and abundant in the middle reaches of Lookout Creek. In accordance with the intermediate disturbance hypothesis, disturbance frequency and intensity may be more moderate in the middle reaches of Lookout Creek, providing suitable conditions for many species including *C. scoparius* and *D. purpurea*.

A wave of invasion: a conceptual model for stream invasion at the Andrews

Figure 30 illustrates a theoretical conceptual model describing the invasion of *C. scoparius* and *D. purpurea* in the Andrews streams. *C. scoparius* and *D. purpurea* were present along roads and in clear-cuts in the Andrews from the 1970s to 2003, but appear to have invaded the stream network only after geomorphic processes in 1996 overcame barriers to stream invasion. Debris flows and flood flows overcame seed dispersal barriers by transporting seeds into the valley

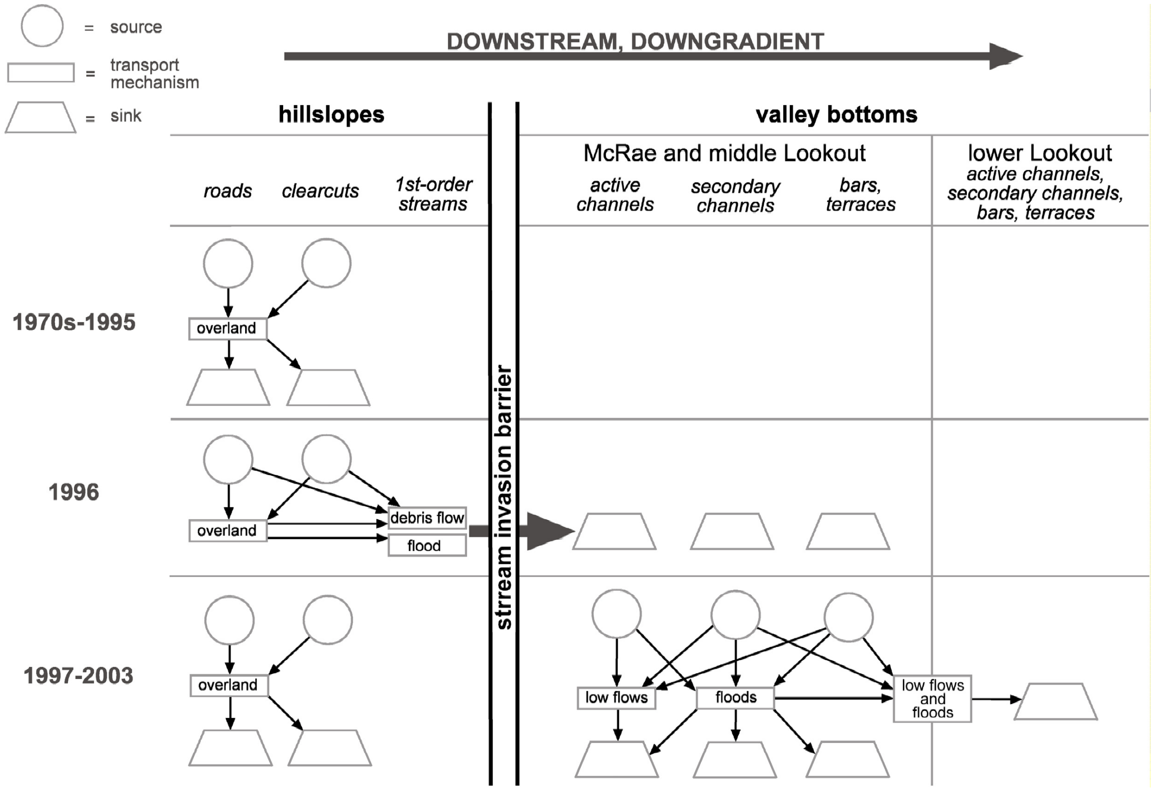

Figure 30. Conceptual model of *Cytisus scoparius* and *Digitalis purpurea* invasion of streams at the Andrews. Geomorphic processes enable the invasion to move from hillslopes to valley bottoms.

bottoms from hillslope source locations along roads and in clear-cut patches. Furthermore, geomorphic processes acting along the stream corridor created suitable conditions for seed deposition, germination, and establishment by removing vegetation and creating sites protected from scour. Seeds were probably deposited in valley bottoms (sinks) away from scour, most likely in middle reaches of the stream network where the unvegetated floodplain was widest and where stream gradient was lowest. Plants probably first became established in these reaches where *C. scoparius* and *D. purpurea* were most frequent and abundant by 2003.

Once geomorphic processes occurring in 1996 had overcome dispersal and establishment barriers and *C. scoparius* and *D. purpurea* had become established along streams, subsequent floods and low flows facilitated redistribution of *C. scoparius* and *D. purpurea* within the stream network. *C. scoparius* and *D. purpurea* patches that probably became established along active and secondary channels and on bars and terraces in lower McRae Creek and in middle Lookout Creek after 1996, could then be sources for downgradient seed transport during low flows between 1997 and 2003 and during flood flows in 1999 and 2000. *C. scoparius* and *D. purpurea* require at least two growing seasons for seed germination and reproduction. As a result, *C. scoparius* and *D. purpurea* invasion patches could not have functioned as seed sources until summer of 1997 at the earliest.

Flood flows after 1997 likely dispersed seeds from sources in middle Lookout Creek into secondary channels and onto bars and terraces within middle Lookout Creek, but also into lower reaches of Lookout Creek. Low flows would not be capable of directly accessing secondary channels and bars and terraces where *C.scoparius* and *D. purpurea* tended to occur in 2003; however, through local autochory and self-dehiscence from the parent plant, source patches could have supplied seeds from locations in secondary channels and on bars and terraces in middle Lookout Creek to the main channel. Low flows could then disperse seeds downstream within the main channel (Figure 30).

CONCLUSIONS

Few studies have addressed the interconnection of road and stream networks in relation to landscape invasions. Exotic species invasions tend to decrease with distance from roads into adjacent landscapes (Parendes 1997, Meekins and McCarthy 2001, Gelbard and Harrison 2003) and bordering landscapes can be "armored" with dense vegetation preventing invasion from roads (Brothers and Springarn 1992). This study shows how extreme geomorphic processes in a steep, forested landscape can facilitate the invasion of *C. scoparius* and *D. purpurea* from hillslope roads and clear-cuts downgradient into streams. Extreme flooding in 1996 connected hillslope seed sources to valley bottoms streams (sinks) and promoted plant establishment in streams by depositing seeds on the floodplain and preparing suitable germination sites by scouring riparian vegetation. Subsequent streamflows (low flows and high flows) have enabled this invasion to propagate down the stream network as a wave of invasion.

Flood magnitude was an important factor in this study, which enabled *C. scoparius* and *D. purpurea* to invade a stream network. Flood frequency and magnitude may be important for sustaining the invasion through local seed dispersal processes and maintenance of a light gap along the stream corridor. However, flood scouring can also cause mortality of an invading plant species. This means that in streams, floods may simultaneously function as a facilitator and barrier to invasion and floods capable of removing riparian vegetation and broadly redistributing seed within the stream network may also eliminate established invasion patches. The spatial and temporal cycles of invasions may behave like invasion waves synchronized with the flood pulse. Without flood disturbance, in time the pattern of *C. scoparius* and *D. purpurea* in the Andrews stream network may break up as post-flood successional vegetation colonizes the stream corridor and conditions in streams become more light-limited. But even in the absence of frequent disturbance, *C. scoparius* and *D. purpurea* will likely remain in the stream network at some level. In this case, they may periodically emerge as waves occurring only after extreme floods when light levels are temporarily increased allowing dormant seeds to germinate and transporting additional seeds from hillslopes into streams. Future monitoring of the *C. scoparius* and *D. purpurea* patch locations along streams at the Andrews will be important in understanding more advanced stages of the plant invasion process in streams.

This study was designed to broadly evaluate the role of geomorphic disturbance in facilitating plant invasions in steep stream networks. Experimental trials targeted a range of processes and patterns that were expected to influence plant invasions in streams. Future studies should focus on more rigorous testing of the effects of seed scarification in different substrate types and at different intensities. Better quantification of the effects of transport processes on seed viability may be useful in understanding the importance of geomorphic transport processes in connecting hillslope seed sources to sinks in valley bottoms. Additionally, further research on seed germination in different substrates and with different amounts of simulated precipitation or with different depths to water, would be helpful in identifying the site characteristics that control invasion locations.

Relationships between invasive plant occurrences and stream characteristics including gradient, unvegetated floodplain width, frequency and abundance of large wood, and propensity for channels to avulse or shift should be better quantified. Exotic plant invasion control efforts are most effectively directed at satellite seed sources called “nascent foci” (Moody and Mack 1988), sinks that have become sources. This means that predicting where invasions are most likely to occur away from the primary seed source in a landscape is very important. With quantitative data relating plant occurrences and stream characteristics, a statistical model can be developed, tested, and applied to predict landscapes most susceptible to invasion. Ultimately this will allow more effective allocation of exotic invasive plant control efforts.

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