ARTICLE

Interactions of sapsuckers and *Cytospora* canker can facilitate decline of riparian willows

Kristen M. Kaczynski, David J. Cooper, and William R. Jacobi

Abstract: Drought has caused large-scale plant mortality in ecosystems around the globe. Most diebacks have affected upland forest species. In the past two decades, a large-scale decline of riparian willows (*Salix* L.) has occurred in Rocky Mountain National Park, Colorado. We examined whether climatic or biotic factors drive and maintain the willow community decline. We compared annual growth and dieback of willows inside and outside of 14-year-old ungulate exclosures and measured groundwater depth and predawn xylem pressures of stems as indicators of drought stress. We also performed an aerial photo analysis to determine the temporal dynamics of the decline. Aerial photo analysis indicated willow decline occurred between 2001 and 2005 and was best explained by an increase in moose population and a decrease in peak stream flows. A new mechanism for willow stem dieback was identified, initiated by red-naped sapsucker wounding willow bark. Wounds became infected with fungus that girdled the stem. DNA analyses confirmed *Valsa sordida* (*Cytospora chrysosperma*) as the lethal fungus. Captured sapsuckers had *V. sordida* spores on feet and beaks identifying them as one possible vector of spread. Predawn xylem pressure potentials remained high through the growing season on all study willows regardless of depth to ground water. Our results indicate that additional mechanisms may be involved in tall willow decline.

Key words: *Cytospora chrysosperma*, Rocky Mountain National Park, *Salix* spp., sapsucker, ungulate, willow.

Résumé : La sécheresse est une cause de mortalité des végétaux à grande échelle dans les écosystèmes sur toute la planète. La plupart de ces dépérissements terminaux ont affecté les espèces forestières des hautes terres. Au cours des deux dernières décennies, un déclin à grande échelle du saule ripisylve est survenu dans le Rocky Mountain National Park, au Colorado. Les auteurs ont examiné si des facteurs climatiques ou biotiques sont responsables et entretiennent le déclin de la communauté des saules. Ils ont comparé la croissance annuelle et le dépérissement terminal des saules à l'intérieur et à l'extérieur d'exclos d'ongulés de 14 ans, et mesuré la profondeur de la nappe phréatique et les pressions du xylème des tiges avant l'aube, comme indicateurs du stress de la sécheresse. Ils ont aussi procédé à une analyse de photos aériennes afin de déterminer la dynamique temporelle du déclin. L'analyse des photos aériennes a indiqué que le déclin des saules est survenu entre 2001 et 2005, et qu'il s'expliquait vraisemblablement par l'augmentation de la population d'orignaux et par la diminution des pics d'écoulement des eaux. Un nouveau mécanisme expliquant le dépérissement terminal des saules a été identifié, initié par des blessures causées à l'écorce des saules par le pic à nuque rouge. Les blessures étaient infectées par des champignons qui entouraient la tige. Les analyses d'ADN ont confirmé que *Valsa sordida* (*Cytospora chrysosperma*) constituait le champignon létal. Les pics à nuque rouge capturés étaient porteurs de spores de *V. sordida* au niveau des pattes et du bec, permettant ainsi de les identifier comme vecteurs possibles de la propagation. Les potentiels de pression du xylème avant l'aube demeuraient élevés tout au long de la saison de croissance chez tous les saules étudiés, indépendamment de la profondeur de la nappe phréatique. Ces résultats indiquent que des mécanismes additionnels peuvent être impliqués dans le déclin des grands saules. [Traduit par la Rédaction]

Mots-clés : *Cytospora chrysosperma*, Rocky Mountain National Park, *Salix* spp., pic à nuque rouge, ongulés, saule.

Introduction

Extreme drought, driven by climate, episodically produces large-scale plant mortality in ecosystems around the globe (Allen et al. 2010). Widespread droughts of the late 20th and early 21st century affected many woody plant species and communities in North America including piñon pine (*Pinus edulis* Englm.) and juniper (*Juniperus monosperma* (Englm.) Sarg.) woodlands in the southwest (Breshears et al. 2005), Englemann spruce (*Picea engelmannii* Parry ex Engl.), lodgepole pine (*Pinus contorta* Douglas), and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) forests in the Rocky Mountains (Bigler et al. 2007), and aspen (*Populus tremuloides* Michx.) forests throughout the Rocky Mountains in the United States and Canada (Anderegg et al. 2012). Species and communities in upland areas have been more severely impacted than in riparian areas (Choat et al. 2012), likely because upland plants rely on soil moisture recharged by precipitation, whereas riparian plants are phreatophytes that use available shallow ground water (Johnston et al. 2011). However, riparian plant diebacks have also been documented. For example, cottonwood (*Populus deltoides* W.Bartram ex Humphry Marshall) dieback has been attributed to river regulation by dams (Rood and Mahoney 1990) or groundwater pumping that created artificial droughts (Cooper et al. 2003). Along low-order rivers, beaver dams that create pools on channels maintain high riparian groundwater levels that may mitigate some drought effects (Westbrook et al. 2006).

Riparian areas comprise a small percentage of western North American landscapes, but provide important ecosystem func-

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tions, including stream bank stabilization, stream water temperature moderation, and habitat for many species of amphibians, reptiles, insects, and mammals (Naiman and Decamps 1997). More than 80% of breeding migratory birds use riparian areas for at least part of their life cycle (Knopf et al. 1988), as well as almost 75% of all vertebrate species (Bunnell and Dupuis 1993), resulting in diverse biota sharing limited resources. The dieback of riparian willows (*Salix* L.) affects many species, especially songbirds; willow stands with stems averaging 0.66 m in height support half the number of avian species and individuals as stands averaging 1.5 m tall (Baril et al. 2011).

In the past 2 decades, riparian willow populations have declined in several regions of western North America, including the Sierra Nevada in California (California Forest Pest Council 2003) and many regions of the Rocky Mountains, including Montana (Limb et al. 2003), Wyoming (Wolf et al. 2007), and Colorado (Peinetti et al. 2002). In Yellowstone National Park, streams that once supported abundant willows 2.5 to 4.5 m in height, beaver dams, and high water tables have been converted to short willow stands because of heavy browsing. Willows now average <1 m tall and are too short for use by beavers (*Castor canadensis* Kuhl) for dam building. The lack of dams has created drier valleys dominated largely by upland plants (Wolf et al. 2007). The interactions of local disturbances, such as ungulate browsing and water table decline due to the absence of beavers, has led to a dramatic alteration of willow stature and population in some areas (Alstad et al. 1999; Wolf et al. 2007). However, these factors alone may not fully explain willow decline.

Drought is a key factor in the decline of many woody plants, and interacting abiotic and biotic factors may also be involved, such as increased ambient air temperatures (Worrall et al. 2010), herbivory (Bilyeu et al. 2008), and insect and fungal pathogen outbreaks (Worrall et al. 2008). The cumulative effects of extreme drought, above average temperatures, high ungulate herbivory, fungal pathogens, and insect attacks are hypothesized to have triggered aspen decline in the western United States (Worrall et al. 2008). An ongoing dieback of thinleaf alder (*Alnus incana* (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung), a common riparian tree in western North America, is linked to high maximum summer temperatures and an epidemic of Cytospora canker (Worrall et al. 2010). The dieback of these two important species has created negative secondary ecological effects such as displaced bird communities (Griffis-Kyle and Beier 2003) and altered nutrient cycling (Nossov et al. 2011). Long (1918) demonstrated that *Cytospora chrysosperma* infected willow stems and this fungi may be an important factor in willow decline.

Red-naped sapsuckers (*Sphyrapicus nuchalis* Baird, hereinafter sapsucker) create distinctive bark wounds, called sap wells, on aspen and tall willow stems >1 cm in diameter to feed on calorie-rich sap. Sapsuckers are keystone species in a sapsucker–willow–aspen – decay fungus community (Daily et al. 1993) as their nest cavities provide habitat for many birds and mammals, including violet green swallows and squirrels, and sap wells are used by many species of mammals, birds, and insects (Ehrlich and Daily 1988). If tall willows are absent, the biodiversity of sap-reliant species decreases (Daily et al. 1993).

The decline of tall riparian willows in the Kawuneeche Valley of Rocky Mountain National Park could be due to possible interactions among native sapsuckers, fungal pathogens, ungulate herbivory, and (or) climate factors. To investigate potential interactions, we used laboratory techniques to identity the fungi present on willows, examined sapsuckers as potential vectors of the fungi, determined the correlation between sapsucker wounding and stem dieback, and examined current climatic variables attributable to current dieback. In addition, we investigated the temporal dynamics of the willow decline using historic climatic, hydrologic, and biotic variables, such as stream flow, snow depth, growing degree days (GDD), precipitation, and elk and moose pop-

ulation estimates. We addressed two primary questions: (*i*) when did the willow decline begin?; and (*ii*) what are the roles of climatic, hydrologic, and biotic drivers in the initiation and maintenance of willow community decline?

Methods

Study area description

Rocky Mountain National Park (RMNP), Colorado, covers 108 000 ha between 2240 and 4345 m in elevation. The average minimum temperature in Grand Lake (elevation: 2554 m) occurs in January (−16.5 °C) and the average maximum temperature in July (24.6 °C). Average annual precipitation for the two stations is 64 cm with most falling as snow (Western Regional Climate Center 2012).

The Kawuneeche Valley study area encompasses 12.5 km of the Colorado River headwaters within RMNP (40°22′N and 105°51′W). It varies from 400 to 1600 m wide. Historically, the Colorado River hydrologic regime was beaver influenced, with dams diverting up to 70% of flow onto floodplains (Westbrook et al. 2006). More than 200 beaver colonies with approximately 1800 individuals occurred in RMNP in 1940 (Packard 1947a); however, a 2009 survey found beaver present at only 17% of historic sites (R. Scherer, Colorado State University, personal communication, 2013). There are no data specifically on beaver populations in the Kawuneeche Valley.

Riparian vegetation is dominated by tall willow species (*Salix monticola* (Bebb), *Salix geyeriana* (Anderson), and *Salix planifolia* (Pursh) are the most common species), which historically averaged 2.5–4.5 m tall (Fig. 1). Meadows are dominated by *Deschampsia cespitosa* ((L.) P. Beauv.) and *Calamagrostis canadensis* ((Michx.) P. Beauv.), and peat-accumulating fens, located on the valley margin, are dominated by *S. planifolia* and *Carex aquatilis* (Wahlenb.). Plant nomenclature follows Weber and Wittmann (2012).

Elk (*Cervus canadensis* Erxleben) and moose (*Alces alces* Gray) are common. Elk populations have increased since they were hunted to near extirpation and reintroduced in the 1910s (Packard 1947b; Lubow et al. 2002), whereas moose were introduced into Colorado in the late 1970s, and their population has rapidly expanded. Both elk and moose browse willows. Willows are an important component of the winter diet of elk (Kufeld 1973; Hobbs et al. 1981), and 90% of moose summer diet is willow (Dungan and Wright 2005). Moose began overwintering in the Kawuneeche Valley during the early 1980s, and the population in 2003 was estimated to be 61 to 66 animals (Dungan 2007). The elk population in the Kawuneeche Valley is not specifically monitored; however, within a game management unit (GMU-E8) that encompasses this valley, the population has been stable since the early 1990s (K. Oldham, Colorado Division of Parks and Wildlife, personal communication, 2012), averaging 2.42 elk·km^{-2} (SD = 0.26 elk·km^{-2}).

Sapsuckers are common throughout the Rocky Mountain region, and their breeding range extends from Arizona and New Mexico north to southeastern British Columbia. They are most abundant in aspen stands. Sapsucker population estimates are not known in RMNP, but in Colorado over the period of 1968–2010, there is an average annual trend estimate of +2.77% (95% credible interval: +1.00% to +4.47%; Sauer et al. 2011).

Aerial photo analysis

True-color aerial photos of the entire Kawuneeche Valley study area for the years 1969, 1987, 1996, 1999, and 2001 were scanned at 1200 dpi. National Agriculture Imagery Program (NAIP) imagery was used for 2005 and 2011 and four band color imagery (color + infrared) was used for 2008. Photo mosaics each year were rectified to the 2005 NAIP imagery using ArcGIS 9.3. The presence or absence of tall willow was analyzed at 25 697 random points generated throughout the floodplain. Willows have a distinct color signature and no other deciduous riparian shrubs could be mistaken for them. We ground truthed the accuracy during summer

Fig. 1. Time series of photographs depicting willow dieback in the Kawuneeche Valley, Rocky Mountain National Park, Colorado. Photographs by D.J. Cooper (1995, 2004, 2008) and K.M. Kaczynski (2012).
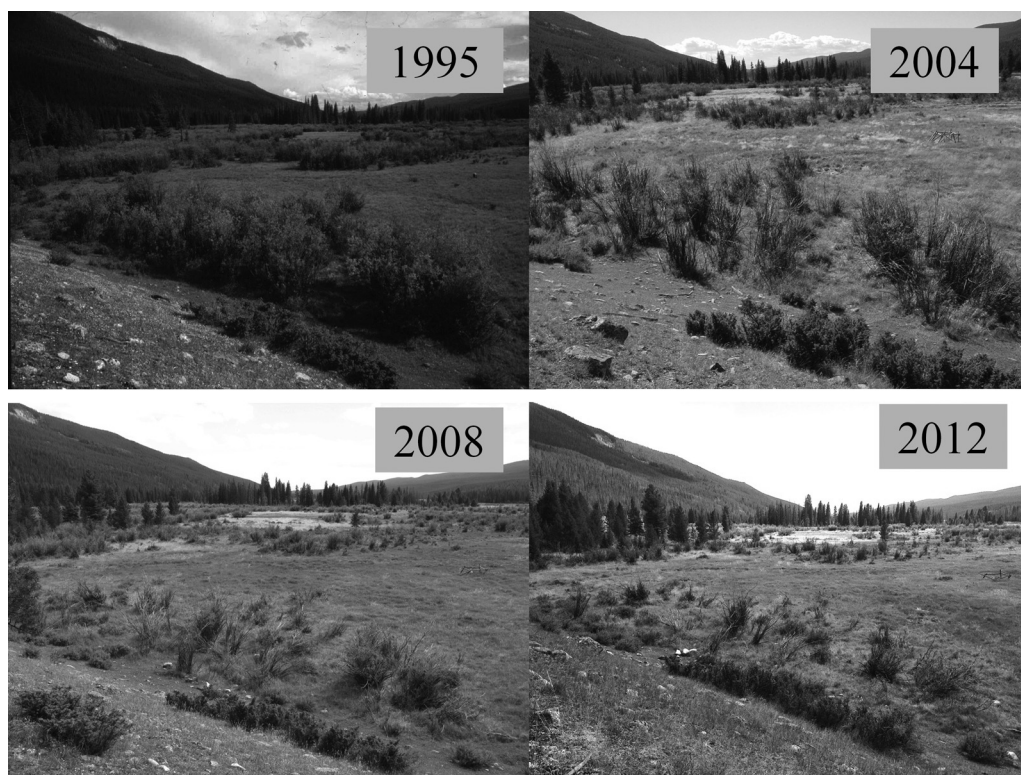
2011 using a double-blind survey of 130 randomly selected points from 2008. Accuracy was 76%. Omission errors were 20%, due to short willows that could not be discerned from the tall herbaceous vegetation, while only 4% were commission errors.

Willow survey

We used three 2500 m² exclosures with 2.5 m tall fences built in 1997 around tall willows to exclude browsing. All exclosures were located in the Kawuneeche Valley in the floodplain of the Colorado River. The most northern exclosure is 7.4 km north of the middle exclosure, which is 3.6 km north of the southernmost exclosure. There is minimal elevational difference among exclosures (average: 2693 m; SD = 44 m).

Five groundwater monitoring wells were installed in 2009 at randomly located sites inside and outside of each exclosure for a total of 30 wells. Around each well, six individual willows ($n = 180$) were randomly selected, tagged, and monitored during 2009–2011. The effects of browsing were measured on the 180 willows, 30 inside and 30 outside each exclosure. In mid-August from 2009 to 2011, we measured the tallest stem to determine plant height and counted live and dead stems. We recorded plant flowering in 2010 and 2011 in early June. Browsing intensity was assessed only in 2011 as an ocular estimate of the percentage of browsed stems using 10% classes on a 0%–100% scale. Current annual growth (CAG) was measured at the end of August in 2009–2011. Stem length and diameter were measured on a subset of stems ($n = 60$) using the methods of Bilyeu et al. (2007). Fifty to 60 stems of each species (*S. monticola*, *S. planifolia*, and *S. geyeriana*) were collected in late August from the study area to develop quantitative relationships between stem length (cm), diameter (mm), and biomass (g) using regression analysis. There were no significant differences among species, which were pooled for analysis ($p = 0.031$). The regression relating log-transformed stem length to log-transformed biomass was used to determine CAG ($r^2 = 0.92$).

Depth to ground water

Depth to ground water was measured biweekly during the 2009–2011 growing seasons (late May – early September) in the aforementioned 30 fully slotted polyvinyl chloride monitoring wells, inside and outside of exclosures. To examine historical groundwater depths throughout the Kawuneeche Valley, we selected 10 additional wells with vegetation surrounding the wells dominated by *S. monticola* or *S. geyeriana*. These depths to water table were previously measured from 1996 to 1998 (Woods 2001) and 2002 to 2004 (Westbrook et al. 2006).

Xylem pressure potentials

Predawn (2300 to 0300 hours) xylem pressure potential (Ψ_{xp}) was measured on current year twigs using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon). Because of time constraints, 60 plants, 30 inside and 30 outside, of two exclosures were measured at the end of June, mid-July, and early August in 2010. Midday Ψ_{xp} was not sampled because of variable cloud cover.

Fungal infection and inoculations

Twenty-five willow stem sections with fruiting fungal pycnidia were collected from the Kawuneeche Valley, placed in humidity chambers to force spore production, and spores were cultured on 1/4 strength potato dextrose agar (PDA)++ media (with antibiotics streptomycin sulfate (0.1 g per 5 mL of H_2O) and chloramphenicol (0.1 g per 2.5 mL ethanol) per 500 mL of liquid media), hereinafter referred to as 1/4 PDA++. The DNA of eight isolates was analyzed using Easy DNA kit Genomic DNA isolation (Invitrogen Corp.) methods (protocol #3) to extract DNA from 10-day-old fungal cultures. We used polymerase chain reaction amplification techniques using internal transcribed sequence universal primers 1 and 4 to enhance amplification of fungi-specific sequence regions (White et al. 1990). Sequencing was performed at the Proteomics

and Metabolomics Facility at Colorado State University. Sequences were matched to known *Valsa* spp. (*Cytospora* spp.) sequences from Gerald Adams (Department of Plant Pathology, Michigan State University), and all sequences identified as *Valsa sordida* Nitschke (anamorph: *Cytospora chrysosperma* (Pers.: Fr.) Fr.) are hereinafter referred to as Cytospora canker.

Field inoculations were performed in September 2010 by creating four circular 8 mm diameter wounds and removing bark. Wounds were approximately 15 cm vertically apart on opposing sides of 14 randomly selected unbrowsed willow stems located within one exclosure. First and third wounds were inoculated with sterile PDA (control), while second and fourth wounds were inoculated with one isolate of *V. sordida*. Isolates used for inoculations were collected from infected stems and cultured on full strength PDA in the laboratory. Canker length was measured in December 2010. Fungi were cultured from all cankers and grown on 1/4 PDA++, and DNA analysis was performed on eight of the recultured fungi.

### Sapsucker stem wounding and bird sampling

We tagged a random selection of *Salix* spp. stems that were wounded by sapsuckers during 2009 ($n = 59$) and 2010 ($n = 55$). Species, length of the wound, stem diameter at the wound, and height of stem were measured during the year of wounding. The following growing season we recorded whether the stem was alive, dead, or dead above the wound but alive below, epicormic shoot development, and presence or absence of Cytospora cankers.

We located nests and captured 9 sapsuckers using mist nests in June 2010 and 2011. The beak and feet of each bird were wiped with sterile cotton swabs that were placed into sterile test tubes with 0.2 mL of deionized water and processed the day of collection. Each swab was streaked four times across two 1/4 PDA++ plates. Swabs were placed in 0.5 mL of deionized water and poured onto two additional plates. Plates were incubated at room temperature for 6 weeks and visually inspected for fungi that were moved onto individual plates to fruit. Plates were stored at 6.5 °C after fruiting to cease growth. DNA analysis was performed on fungal cultures resembling *V. sordida*.

Statistical analyses

We estimated parameters to explain willow decline over time, as determined by the aerial photo analysis, using change-point regression. Using R version 2.9.3 we determined where the change point occurred in the data and modeled the data before and after the change point. Hydrologic and climatic variables included average stream flow, average stream flow 1 and 2 years prior, peak stream flow, peak stream flow 1 and 2 years prior, total water year precipitation and 1 year prior, total snowfall accumulation, and GDD. Stream flow data were obtained from the USGS stream gage along the Colorado River below Baker Gulch (USGS 09010500). Precipitation data were obtained from the Phantom Valley SNOTEL site. Temperature data were obtained from the Grand Lake climate station (Western Regional Climate Center 2012). We used a threshold of 5 °C to calculate GDD to obtain an estimate of growing season length. Peak and average stream flows (Pearson's $r = 0.88$), snow depth and peak stream flow (Pearson's $r = 0.75$), snow depth and average stream flow (Pearson's $r = 0.80$), and snow depth and precipitation (Pearson's $r = 0.86$) were highly correlated; therefore, only one measure of each was used in each model. Elk population data for the E8 GMU, which includes the western part of RMNP, were obtained from the Colorado Division of Parks and Wildlife. No data are available for moose population size in specific GMUs; therefore, the number of hunting tags allowed per year in each GMU was used as an estimate of moose populations (Boyce et al. 2012). The number of hunting tags is determined by hunter success, antler spread, non-hunter mortality, and illegal mortality and has increased as the population has increased (K. Oldham, Colorado Division of Parks and Wildlife, personal communication, 2012). Moose hunting began in the

Fig. 2. Willow presence points (surrogate for willow cover) in the Kawuneeche Valley study area from 1969 to 2011. Triangles are years of aerial photo analysis.
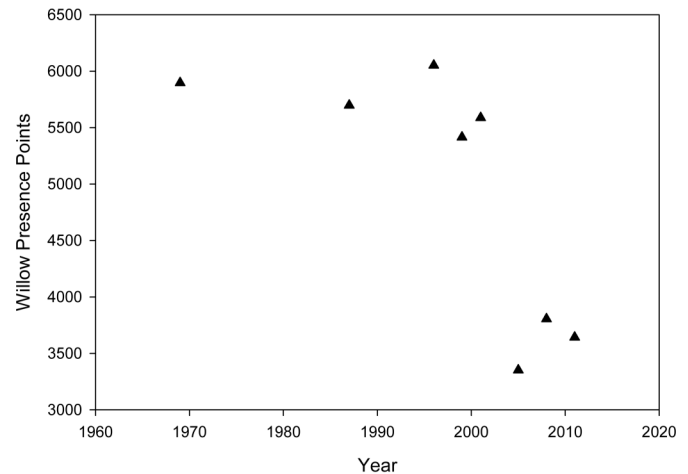
GMU-E8 in 1995 when four licenses were issued and increased linearly to 29 in 2011 (Pearson's $r = 0.93$). Hunter success is 85% (K. Oldham, Colorado Division of Parks and Wildlife, personal communication, 2012). Biological variables included in the model were elk population in the year of the aerial photo and 1 year prior, the number of moose hunting tags issued in the year of the photo and 1 year prior, and the presence or absence of beaver (as the presence or absence of beaver dams). Models were ranked using corrected Akaike's information criterion (AIC_c) (Burnham and Anderson 2002).

Log-transformed stem height and CAG were analyzed using generalized linear mixed models for each growing season, with exclosure as a random effect. Fixed effects in each model tested browsed versus unbrowsed plants and depth to water table in late July, as well as possible two-way interactions. We used ANOVA to test for differences in CAG among species, with a Tukey's HSD (honestly significant difference) test to adjust for unequal group sample sizes. Ψ_{xp} was analyzed using generalized linear repeated measures mixed models.

Stem death from sapsucker wounding was modeled using logistic regression with stem height, length of wound, stem diameter at the wound, and species as predictor variables. We investigated possible two-way interactions. We used ANOVA models to compare inoculated and control canker sizes. Effect size (η^2) is reported.

A maximum-likelihood-based model selection framework was used to evaluate competing models, using AIC_c (Burnham and Anderson 2002). We examined deviance explained by the model compared with a null model (a model with only an intercept) to determine model strength and reported this as the variance explained. All analyses were done using R version 2.9.2 (R Development Core Team 2008), with packages nlme, lmm fit, and MASS.

Results

Aerial photo analysis

Tall willow cover in the Kawuneeche Valley decreased by approximately 40% between 2001 and 2005 (Fig. 2). Change-point regression models performed better than models not including a change point. Change points occurred between 2001 and 2005 for all models. The best model included the number of moose hunting tags issued and the previous year peak stream flow and had an AIC weight of 0.87, indicating 87% of the weight of evidence favored this model over all other candidate models. This model explained 99% of the deviance over the null model. The presence of willow was positively associated with peak flow and negatively associated with moose hunting tags.

Fig. 3. Depths to ground water during wet and dry years in the Kawuneeche Valley, Rocky Mountain National Park, Colorado. Dominant vegetation at each well was *Salix geyeriana* or *Salix monticola*. n = 10 for each time period. Error bars are ± 1 SD from the mean.
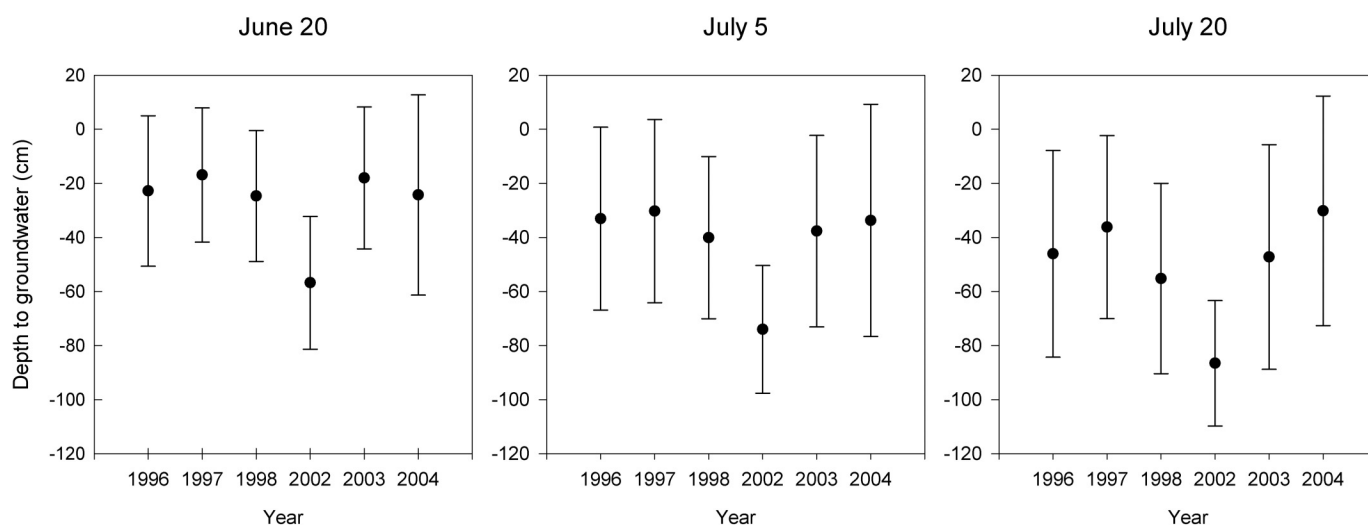
Groundwater levels and drought stress

Depth to ground water in the Kawuneeche Valley over the past 15 years averaged 20 cm in late June and 50 cm in late July for all years except 2002, when it averaged 58 cm in late June and 85 cm in late July (Fig. 3) (Woods 2001; Westbrook et al. 2006). Colorado River discharge in 2002 was one of the lowest on record, yet average groundwater depths never exceeded 1 m. These depths are well within the rooting depth of the study willow species.

Mid-July groundwater depths during 2009 to 2011 in the exclosures ranged from 0 to more than 160 cm below the ground surface. Depth to ground water was not a statistically significant predictor of stem height in any study year (p = 0.856) and was similar in browsed and unbrowsed areas (p = 0.536).

Predawn Ψ_{xp} for all willows averaged −0.091 MPa (SD = 0.04), −0.21 MPa (SD = 0.07), and −0.084 MPa (SD = 0.04) in late June, mid–July, and early August, respectively. There were no significant differences among sample periods (p = 0.32) or between browsed and unbrowsed plants (p = 0.82).

Browsing, willow heights, and CAG

Unbrowsed willow stems averaged 209 cm (SD = 4 cm) from 2009 to 2011 and were significantly taller than browsed stems that averaged 82 cm (SD = 2 cm) (p < 0.01) (Fig. 4), and browsed willows, regardless of browsing intensity, were shorter than unbrowsed willows. The presence of browsing best explained willow height in 2009, 2010 (Table 1), and 2011, explaining 70%, 69%, and 71% of the variation, respectively, over the null models. The average number of live stems greater than 150 cm tall was one per plant (SD = 3) outside of exclosures and 15 per plant (SD = 16) inside exclosures. An average of 17 dead stems (SD = 12) occurred on plants outside exclosures and 7 (SD = 8) on plants within exclosures.

CAG was greater for unbrowsed than browsed stems (p < 0.01) (Fig. 4) in all years. Stem height (model 1) and height and browse intensity (model 2) best explained 2011 annual growth, accounting for 43% to 53% of the variation (Table 1). In 2009 and 2010 stem height and the presence of browsing best explained CAG, accounting for 70% and 58% of the variation, respectively. Depth to ground water in mid-summer and species identity were not predictors of CAG in either year. Only 3% of browsed plants flowered, thus the sex of most plants could not be identified or used as a model variable, whereas 93% of unbrowsed plants flowered.

Cytospora canker infection

Valsa sordida (*C. chrysosperma*) inoculated cankers averaged 18 mm in length (SD = 8 mm) after 3 months and were significantly larger than controls, which averaged 10.7 mm (SD = 0.65 mm) (p < 0.01, η^2 = 0.45). Cankers expanded on 57% of inoculated wounds and on none of the control wounds. Re-isolation and DNA analysis of fungi from six of the eight sampled cankers were identified as *V. sordida*.

Eleven fungi, yeast, and bacteria species were identified in cultures from sapsucker beaks and feet. Six cultures had fruiting bodies identified as *V. sordida*, three from feet and one from a beak. *Valsa sordida* was found on one-third of the captured birds, indicating that sapsuckers are a possible vector for *V. sordida* dispersal.

Stem wounding by sapsuckers

Sapsuckers used tall willow stems 7.5 to 24.4 mm in diameter (mean 13.8 mm, SD = 2.6 mm; n = 115). Wounded stems averaged 237 cm tall and all were inside exclosures because stems outside exclosures were of insufficient diameter (mean 7.5 mm, SD = 1.6 mm; n = 90) or height (mean 81 cm, SD = 28 cm) for sapsucker use. Stem mortality occurred above sapsucker wounds on 47% and 62% of stems in 2009 and 2010, respectively. Logistic regression models indicated an increase in wound length was the most important variable explaining stem death. Cytospora canker infection rates of 93% and 100% occurred on stems that died in 2010 and 2011, respectively. Sapsucker wounds were an average of 82 cm above the ground surface, and stem death above the wound triggered by sapsucker resulted in live stems averaging 85 cm tall (SD = 20 cm). The heights of these resulting stems were not significantly different than stem heights maintained by ungulate browsing (p = 0.63). Epicormic shoots formed below the wound on 68% of stems in 2009 and 2010.

Discussion

The decline of many upland forest communities has been linked to drought, native and exotic diseases, or insect epidemics (Breshears et al. 2005; Allen et al. 2010). Our aerial photo analysis of tall willow cover decline in the Kawuneeche Valley was best explained by lower peak stream flows and an increase in moose. We present a new mechanism for willow decline in RMNP, driven by three interacting low intensity stressors: sapsucker wounding, fungal cankers, and repeated ungulate browsing of epicormic shoots. We identified sapsuckers as a potential vector for the fungi, which infects and kills willow stems, entering through the sapsucker wounds. Inside exclosures, we observed epicormic shoots initiating below wounds have the potential to grow tall because of the absence of browsing, perpetuating tall willow com-

Fig. 4. Comparison of the mean of willow height (cm) and annual growth (kg·plant⁻¹) for 2009, 2010, and 2011. Plants in the Kawuneeche Valley, Rocky Mountain National Park, Colorado, outside exclosures are browsed and plants inside are unbrowsed. Sample sizes for heights: browsed, $n = 30$; and unbrowsed, $n = 30$. Sample size is 15 for year of annual growth.
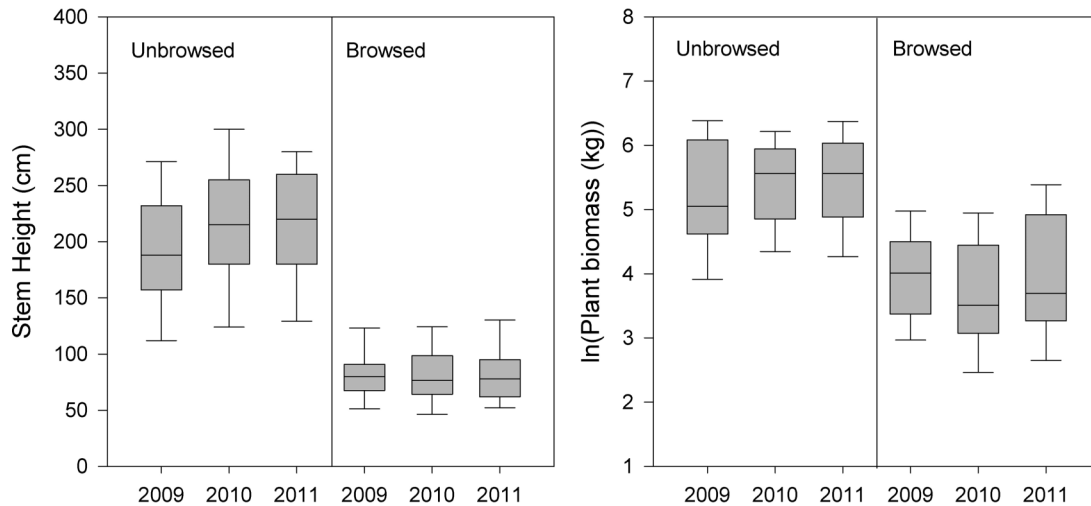

Table 1. Model comparisons based on AIC_c for explaining willow stem height (cm) and current annual growth (g) in 2011 for the Kawuneeche Valley study area.

Model ranking	k	AIC_c	ΔAIC_c	Model weights	Variance explained
Willow stem height					
Browsed	2	256.89	0	0.99	0.52
Browsed + water table	3	267.64	10.75	0.005	0.53
Browsed*water table	4	279.65	22.76	0	0.54
Water table	2	378.58	121.69	0	0.02
Current annual growth					
Height	2	147.54	0	0.49	0.43
Height + browse intensity	3	148.45	0.91	0.31	0.53
Height + browse intensity + browsed in 2010	4	149.86	2.32	0.15	0.53
Browse intensity	2	152.24	4.7	0.05	0.49

Note: 2011 models had identical model weights when compared with 2010 models. k is the number of parameters in the model. AIC_c is the corrected Akaike's information criterion. Model weight is the Akaike weight and represents the relative likelihood of the model. The variance explained is the amount of variance explained over the null model. All models included exclosure as a random effect. Water table is the July depth to the water table (cm). "Browsed" is a binary variable. Height is height of the tallest stem on an individual plant in centimetres. "browsed in 2010" is a binary variable and browse intensity is a class variable, 0%–100% scale, at 10% intervals for each plant in 2011.

munities. Outside exclosures, browsing created short willows that were insufficient in height and diameter for sapsucker use, in addition to beaver and songbirds (Naiman and Decamps 1997; Baril et al. 2011). We propose that in the presence of high ungulate browsing, sapsucker wounding and Cytospora cankers can kill the stems and trigger willow height decline and ungulates maintain short stature willows through the browsing of epicormic shoots.

Historic analysis

Climatic and hydrological drivers may have played a role in the initiation of the tall willow dieback. Peak flow the year prior to when the aerial photo was taken, along with moose population estimates, was a significant variable explaining the decline in tall willow cover. The years the sharp decline in willow cover occurred had higher moose population estimates and lower previous year peak stream flows, suggesting possible drought conditions. However, willow communities with active beaver dams that raise stream stage and support high floodplain groundwater levels may not experience the hydrologic effects of prolonged drought. Westbrook et al. (2006) showed that in the low stream flow years 2002 and 2004, when our aerial photo analysis indicated a sharp reduction in willow cover, a much larger area of the Kawuneeche

Valley floodplain was inundated late in the summer by beaver dams than in 2003, when beaver dams were washed out of the channel by a large flood. In addition, most of the floodplain had water tables closer to the soil surface and flooding occurred longer in the drought years when the dams were in place. Beavers have not been present in the Kawuneeche Valley since 2005 because short willows provide inadequate food and dam building material. However, predicted warmer average annual temperatures and earlier peak stream flow (Stewart et al. 2005) could influence willow growth and physiology in the future, as beavers are not present to mitigate the low peak flows. In addition, climate change research predicts that more precipitation will fall as rain rather than snow (Regonda et al. 2005). In 2002 and 2004, the total monsoonal rain (July and August) was 13.7 cm and 15.0 cm, respectively, above the 30 year average of 10.7 cm (SD = 3.4 cm). This could also alter the dynamics of the willow community.

A fundamental difference in riparian willow and upland forest tree species decline is due to willows being phreatophytes whose primary water source is shallow ground water (Johnston et al. 2011). Willows are moderately susceptible to drought stress; however, when they have access to a reliable source of ground water <3 m from the ground surface, they rarely experience hy-

Fig. 5. Conceptual diagram describing the relationships among ungulate browsing, beaver occupation, sapsucker use, and fungal infection on riparian willow communities.
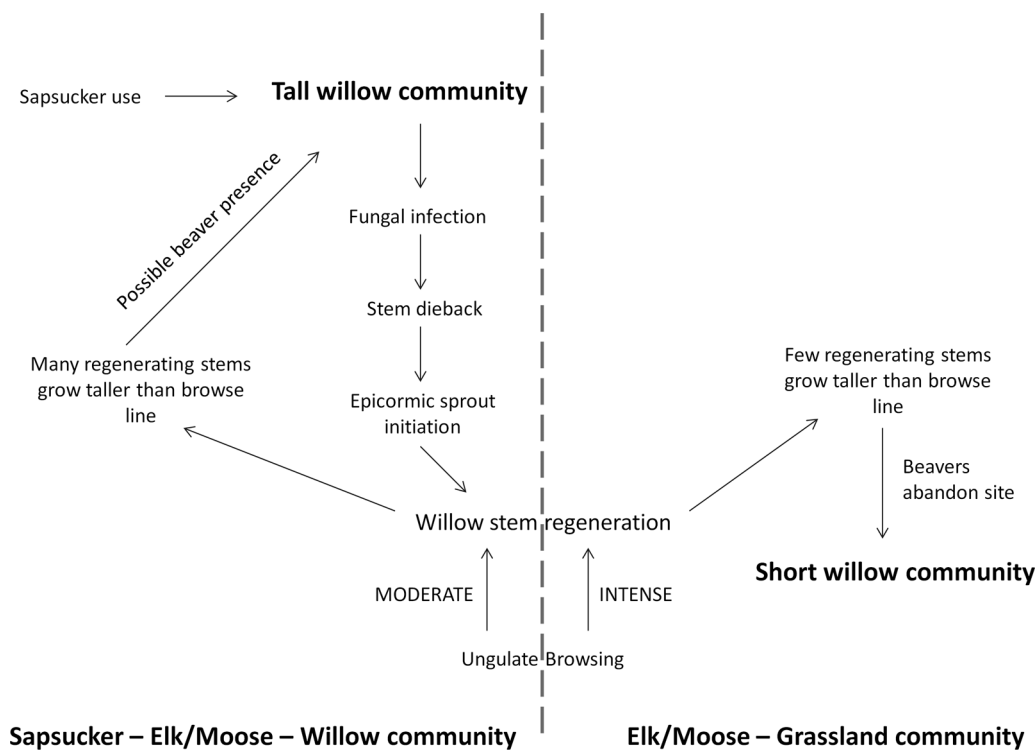
draulic failure (Horton et al. 2001). In contrast, upland plants rely on precipitation-driven soil water and experience hydraulic failure due to xylem cavitation during drought. Aspen branches exhibit a 50% loss of hydraulic conductivity at a Ψ_{xp} of −1.1 to −2.5 MPa (Hacke et al. 2001), whereas willows exhibit a 50% loss of conductivity between −1.57 and −2.18 MPa (Johnston et al. 2007). Aspens are more vulnerable to drought-induced cavitation because nightly Ψ_{xp} recovery is limited by soil water availability (Anderegg et al. 2013). Willows have rapid nighttime recovery from daytime water potentials, sometimes exhibiting a higher Ψ_{xp} than Ψ_{soil} during predawn measurements, indicating that roots access ground water (Foster and Smith 1991). Predawn Ψ_{xp} in 2010 was high in all study willows regardless of groundwater depth. Midday Ψ_{xp} of willows can also be high. During the 2004 drought year willow stem Ψ_{xp} averaged −1.3 MPa in mid to late August in Yellowstone National Park (Johnston et al. 2007). Approximately 77% of water used by willows in RMNP is ground water (Alstad et al. 1999). Willows use soil water when it is available early in the growing season and deeper ground water later in the summer (Johnston et al. 2011). Groundwater use by willows in Yellowstone National Park was not correlated with water table depth, and plants consistently used primarily ground water at sites with a water table deeper than 140 cm (Johnston et al. 2011).

The number of GDD was not an important factor in the willow decline; however, increased winter temperatures could also play a role in the future. Temperature has large effects on fungal infection, and strains of *Cytospora* spp. have been documented to grow at temperatures as low as 3 °C (Helton and Konicek 1962).

Role of sapsuckers

Sapsucker use of willow stems in North America has been known for more than a century (McAtee 1911). In western Colorado, Ehrlich and Daily (1988) reported that sapsucker impacts on willow stems were "severe, and probably greater than that of any other herbivore that feeds on willows in the summer". They observed that 72% of willow shrubs had severely damaged stems and

within a shrub, an average 28% of stems were damaged and 98% of damaged stems were dead (Ehrlich and Daily 1988). The researchers did not examine how long after wounding stems died and noted that recent sapsucker damage was apparent until approximately 5 years after their death when stems had lost their bark and the characteristic patterning of sapsucker wounding was lost. Fungal infection was not implicated in the stem death. In RMNP, 47% and 62% of stems wounded by sapsuckers in 2009 and 2010, respectively, were dead within 1 year indicating high stem mortality from sapsucker use. Sapsucker wounds are the entry point for Cytospora spores that form lethal cankers. Sapsucker-initiated stem dieback reduced willow heights to less than 1 m, similar to the height maintained by ungulate browsing. A key difference between RMNP and sites investigated by Ehrlich and Daily (1988) was the low level of ungulate browsing in their sites (C. Floyd, Rocky Mountain Biological Lab, personal communication, 2012). Willow stems died at their study site, yet the formation and growth of unbrowsed epicormic shoots allowed stems to regain their original height in a few years, facilitating the long-term persistence of tall willow communities. In contrast, resprouting epicormic shoots in RMNP could be browsed by moose and elk creating and maintaining a short willow community.

Fungal infection

Cytospora spp. are facultative wound pathogens requiring physical damage to bark, such as sap wells, to infect plants. Once present on a wound, hyphae grow through the phloem and xylem killing the stem above the wound (Biggs et al. 1983). Drought-stressed plants are thought to be more prone to Cytospora canker (McIntyre et al. 1996). However, we found that 57% of wounded and inoculated stems with canker expansion had low predawn Ψ_{xp} during the summer (K.M. Kaczynski, unpublished data) indicating that drought stress was not a precursor for Cytospora canker growth and expansion (Kaczynski and Cooper 2013).

Cytospora chrysosperma is implicated in the widespread aspen decline in the western United States (Worrall et al. 2008). However

the linkage among sapsuckers, *C. chrysosperma*, and willows has been undocumented. Sapsuckers preferentially create cavity nests in aspens, often in close proximity to willow stands and use willows throughout their breeding season (Daily et al. 1993). While *C. chrysosperma* spores can be wind and rain dispersed, sapsuckers also facilitate spore movement from aspen to willow during trips from nests to feeding sites. Migratory birds are known to carry spores on their feathers and feet (Warner and French 1970), and birds in the eastern United States carried chestnut blight spores in high numbers (Heald and Studhalter 1914).

Role of browsing in maintaining willow height

In the absence of predators, elk and moose populations have increased in RMNP detrimentally affecting riparian communities. Peinetti et al. (2002) concluded that willow decline in RMNP was "clearly associated with an increase in elk abundance". Willow stems greater than 200 to 250 cm tall are thought to be above the reach of browsing elk and moose (Keigley et al. 2002). Willow stems outside exclosures in the Kawuneeche Valley averaged 82 cm indicating all unexclosed willows are within the reach of browsers. Only 3% of willows outside of exclosures were not browsed in 2011. Although willows are resilient to ungulate browsing, CAG was significantly higher on unbrowsed stems in all years and annual browsing reduced their productivity and maintained their short stature.

Baker et al. (2005) proposed that when beavers cut willow stems nearly to the ground, ungulate browsing removed resprouting shoots to maintain short stature willows. Here we demonstrate that sapsuckers can facilitate Cytospora canker infection, which in the presence of high ungulate browsing, could produce short willow stands.

Alternate cause for decline of willow populations

Sapsuckers, Cytospora canker, ungulates, beaver, and high snow years resulting in high peak stream flows are components of functioning willow ecosystems in the Rocky Mountains (Fig. 5). Under a scenario of low to moderate browsing, the majority of willows have some live tall stems, beavers have access to willows suitable for food and dam building, and sapsucker use is dispersed by the large populations of tall willows. Cytospora canker infects and kills wounded or stressed stems, but epicormic shoots have the potential to grow to full height maintaining a tall willow community. Under high browsing pressure, the majority of willow stems are short and unsuitable for beavers, and sapsucker use is highly concentrated on willows with larger diameters and taller stems, exacerbating the dieback. Without beaver dams widespread water table declines occur in the riparian zone. The loss of epicormic shoots to browsing produces a bottleneck in the long-term maintenance of willow-dominated riparian ecosystems.

A diverse group of species relies on riparian ecosystems for survival, yet their disturbances have facilitated the willow decline. As tall willow stands became rarer, species use became more concentrated on the remaining willows creating rapid change in height. Our understanding of these interactions allows land management agencies to develop appropriate and effective restoration strategies. Long-term recovery and survival of a willow community could require a reduction in ungulate browsing by population reduction or fencing. Only actions that would allow epicormic shoots to regrow and restore willow height can facilitate riparian ecosystem recovery and support beaver and other important elements of mountain region biodiversity.

Acknowledgements

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Appendix A

Table A1. Coefficients, standard errors, and 95% confidence intervals of the highest ranked models for each analysis in manuscript.

Variable	Coefficient	Standard error	95% confidence interval	
Aerial photo analysis of willow decline: generalized linear model with a change point				
Intercept	8496	58.38	8381.52	8610.37
X < change point	−2964	68.12	−3098.003	−2830.97
X > change point	975.3	14.4	947.023	1003.479
Previous year peak flow	0.918	0.015	0.889	0.948
Moose	46.19	0.981	44.267	48.114
Stem height (2011) generalized linear mixed effect model with a random effect for exclosure				
Intercept	5.345	0.075	5.258	5.502
Browsed	−1.079	0.082	−0.918	−1.240
Current annual growth (2011) generalized linear mixed effect model with a random effect for exclosure				
Intercept	−2.025	0.959	−4.261	−2.569
ln(stem height)	1.361	0.184	1.721	−0.519
Sapsucker stem wounding: logistic regression predicting stem death				
Intercept	1.954	0.456	1.112	2.912
Wound length	−0.357	0.072	−0.513	−0.228