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Shrub expansion over the past 62 years in Rocky Mountain alpine tundra: possible causes and consequences

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Abstract

Woody plants are encroaching into many herbaceous-dominated communities across the globe, including arctic and alpine tundra. Quantifying the encroachment rate, testing which factors contribute to encroachment, and determining how encroachment is taking place and in which community types encroachment is occurring are essential for predicting shifts in tundra vegetation and carbon (C) storage. We examined willow cover changes from 1946 to 2008 in 18 ha of alpine tundra in Colorado using aerial photographs. We linked this pattern of change with experimental assessment of the effects of increasing summer temperatures, winter precipitation, and nitrogen (N) deposition—factors that this region has experienced over this period—on willow growth and survival. Shrub cover expanded by 441% over 62 years and is increasing at an exponential rate, corresponding to increases in C storage of 137 kg ha⁻¹. Nitrogen and temperature facilitate willow growth and snow increases survival, although N and the combination of N plus snow decrease survival. We find clonal growth (78%) accounts for more expansion than seed dispersal (22%), and that shrubs have expanded into wet, moist, and dry meadow. In addition to a release from grazing, we suggest that global change could be driving shrub expansion.

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Introduction

Woody plants are encroaching into many herbaceous-dominated communities across the globe, including arctic and alpine tundra (Sturm et al., 2001; Stow et al., 2004; Tape et al., 2006; Cannone et al., 2007; Hallinger et al., 2010; Myers-Smith et al., 2011a; Rundqvist et al., 2011). However, there are many proposed causes and consequences of this drastic change in functional composition, from herbaceous-dominated to woody-dominated, which have been widely discussed and difficult to test (Myers-Smith et al., 2011b). Understanding causes and consequences of woody encroachment is essential for predicting future change in tundra vegetation and informing management and policy decisions.

Global change is often cited as a major cause of woody encroachment in arctic and alpine tundra. Increases in woody plant species in the arctic tundra observed over decadal time scales are often associated with climate warming over the same period (Chapin et al., 2005; Weintraub and Schimel, 2005). Experiments across tundra sites worldwide have shown that warming treatments enhance shrub cover and vegetation height (Walker et al., 2006; Elmendorf et al., 2012a). The effect of warming on shrub increase is especially strong for deciduous shrubs growing in wet regions (Elmendorf et al., 2012b). Manipulative experiments have shown that shrubs benefit at the expense of herbaceous vegetation from increases in soil nutrients (Bret-Harte et al., 2002; Hobbie et al., 2005), which could occur either directly through nitrogen (N) deposition or indirectly through stimulation of microbial decomposition by warming (Chapin et al., 1995; Hobbie et al., 2002) or increased snow cover (Schimel et al., 2004). Dispersal limitation of

encroaching woody plants and the competitive ability of the community types into which they are dispersing can both limit or facilitate woody establishment (Dullinger et al., 2003). In the arctic, evidence suggests that increased snowpack depth and duration favors the expansion of shrubs (Sturm et al., 2005b; Weintraub and Schimel, 2005).

Changes in land use, particularly grazing by native ungulate species such as elk and caribou and agricultural species such as sheep and cattle, can also affect woody encroachment. Observational studies suggest that herbivory can constrain treeline advance into alpine zones (Cairns and Moen, 2004; Van Bogaert et al., 2011), and shrub growth occurs more rapidly inside exclosures shortly after grazing cessation (Chadde and Kay, 1991; Holland et al., 2005; Speed et al., 2013). Once established, selective feeding by herbivores on grasses with high nutrient content may maintain existing shrub patches (Jewell et al., 2005). Moreover, long-term experiments in the alpine (Hofgaard et al., 2010) and arctic (Post and Pedersen, 2008; Olofsson et al., 2013) find that woody plant responses to grazing removal are stronger than responses to increased temperatures or that they interact with one another. Attributing causation to climate–woody encroachment correlations may be misleading if land-use history is not considered.

No matter what the cause, woody encroachment has major consequences for ecosystem function in the tundra. Studies show that arctic shrubs typically increase N cycling (Mack et al., 2004; Sturm et al., 2005b; Weintraub and Schimel, 2005). Similarly, woody shrubs substantially increase the amount of carbon (C) stored in recalcitrant woody biomass, which can have consequences for C cycling (Walker et al., 1993; Shaver et al., 1998; Myers-Smith et al., 2011b). The structural properties of

shrubs elevate winter soil temperatures by trapping snow, which results in more decomposition (Sturm et al., 2005b). Shrubs are also expected to cause a net decrease in both summer and winter albedo, increasing summer and winter temperatures. Expanding shrubs replace lighter-colored tundra vegetation, decreasing summer albedo (Chapin et al., 2005). Increased shrub height and density also decrease winter albedo because stems protrude through the snow (Sturm et al., 2001). Despite trapping snow (which could potentially increase the duration of snow cover and increase albedo), studies show that shrubs and tundra vegetation have similar melt-out dates because shrub areas start melting earlier (Sturm et al., 2005a, 2005b). Overall, lower albedo along with increased N and C cycling and soil temperatures may generate positive feedbacks, further accelerating encroachment (Sturm et al., 2001, 2005b).

While most research has focused on arctic tundra or treeline in higher latitudes, here we focused on whether similar dynamics occur on Niwot Ridge, a high-elevation alpine site in the Front Range of the Rocky Mountains. Niwot Ridge is experiencing increasing temperatures, winter precipitation, and N deposition (Fig. 1), and also has a history of intensive sheep grazing prior to the late-1940s (Marr, 1964). We first investigated expansion rates from a 62-year time series of aerial photographs from 1946 to 2008. Next, we explored willow response to global change factors (N, snow, and temperature) by examining survival and growth of seedlings in a manipulative field experiment. To understand the dynamics of willow expansion and consequences for the tundra ecosystem, we used the aerial photograph series to quantify the amount of willow expansion due to clonal growth versus new patch formation (colonization by seed). We also combined the aerial photograph data and a vegetation map of Niwot to identify the tundra community types most susceptible to invasion. Finally, we assessed the consequences of willow invasion for C storage using tissue C content and biomass of shrubs versus herbaceous tundra vegetation.

Methods

SITE DESCRIPTION

This study was conducted on Niwot Ridge at an elevation of 3500 m, located in the Colorado Front Range of the Rocky Mountains about 5 km east of the Continental Divide and 35 km west of Boulder, Colorado (40°03'N, 105°35'W) (Fig. 2). Niwot Ridge is an alpine tundra site that is part of the Long Term Ecological Research (LTER) network. Climate is characterized by long, cool winters and a short growing season that lasts 1–3 months between May and August. It has a mean summer temperature of 5.5 °C, mean winter temperature of –12.7 °C, and a mean annual precipitation of 993 mm (from 1961–1990, Greenland and Losleben, 2001). Most precipitation falls as snow during the winter and spring months and is redistributed by strong winds (10–13 m s^{–1}), causing snow depth to vary with distance by a factor of 10 or more (Greenland, 1989). Soils are approximately 2.0 m in depth over granitic parent material (Burns and Tonkin, 1982). Tundra vegetation on Niwot Ridge is classified as dry, moist, and wet meadow communities, fellfield communities, snowbeds, and shrub tundra (May and Webber, 1982). The two tall shrub willows that are encroaching in the tundra are *Salix planifolia* Pursh and *Salix glauca* L. Both species have wind-dispersed seeds but can also be dispersed by animals and water and can spread clonally via lateral shoots.

Our focal region on Niwot Ridge is the Saddle, an experimental site divided into 88 grid points (8 × 11), each separated by about 50 m, with an area of 178,497 m² (Fig. 3). It is situated on a ridge-top, traversing a shallow low area between two knolls on the eastern and western sides. The grid encompasses points in all alpine tundra

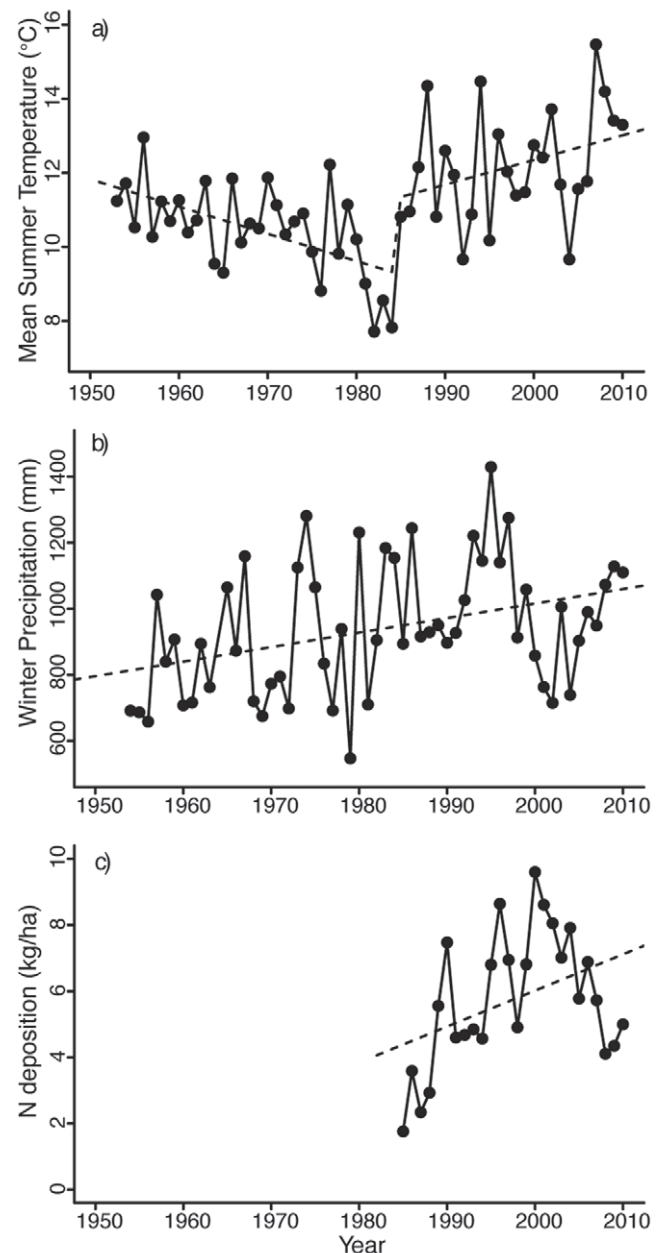


FIGURE 1. (a) Mean summer (June–August) temperature trend from 1953 to 2010, (b) winter precipitation (September–May) from 1954 to 2010, and (c) annual N deposition 1985–2010. There is a significant decrease in summer temperature during the first half of the time period and an increase in temperature during the second half of the time period (fit with a piecewise regression, $R^2 = 0.438$, $F = 13.445$, $P < 0.001$). There is a significant increase in precipitation and N deposition over time: winter precipitation ($R^2 = 0.136$, $P = 0.005$), N deposition ($R^2 = 0.170$, $P = 0.036$). Temperature and precipitation data are from the D1 weather station at Niwot Ridge, approximately 2.4 km from the Saddle study site. N deposition is measured in the Saddle.

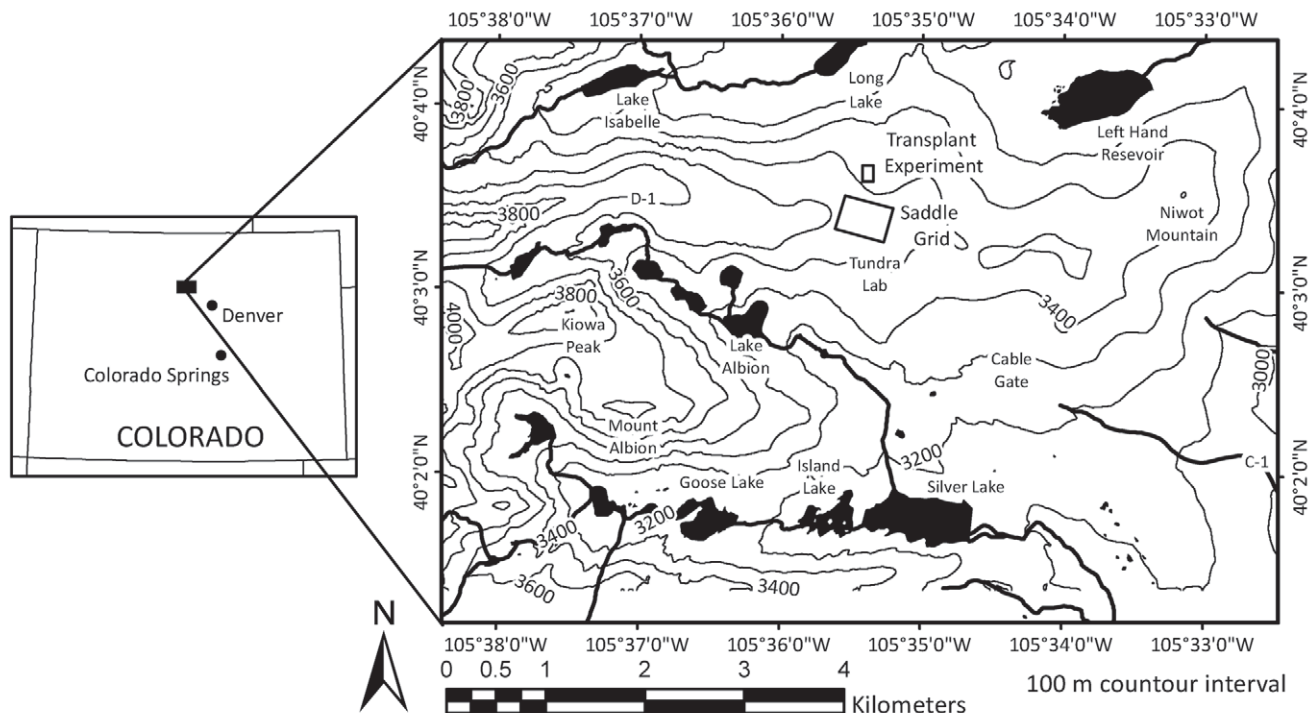


FIGURE 2. Site map of Niwot Ridge, Colorado, showing the locations of the Saddle and Salix transplant experiment.

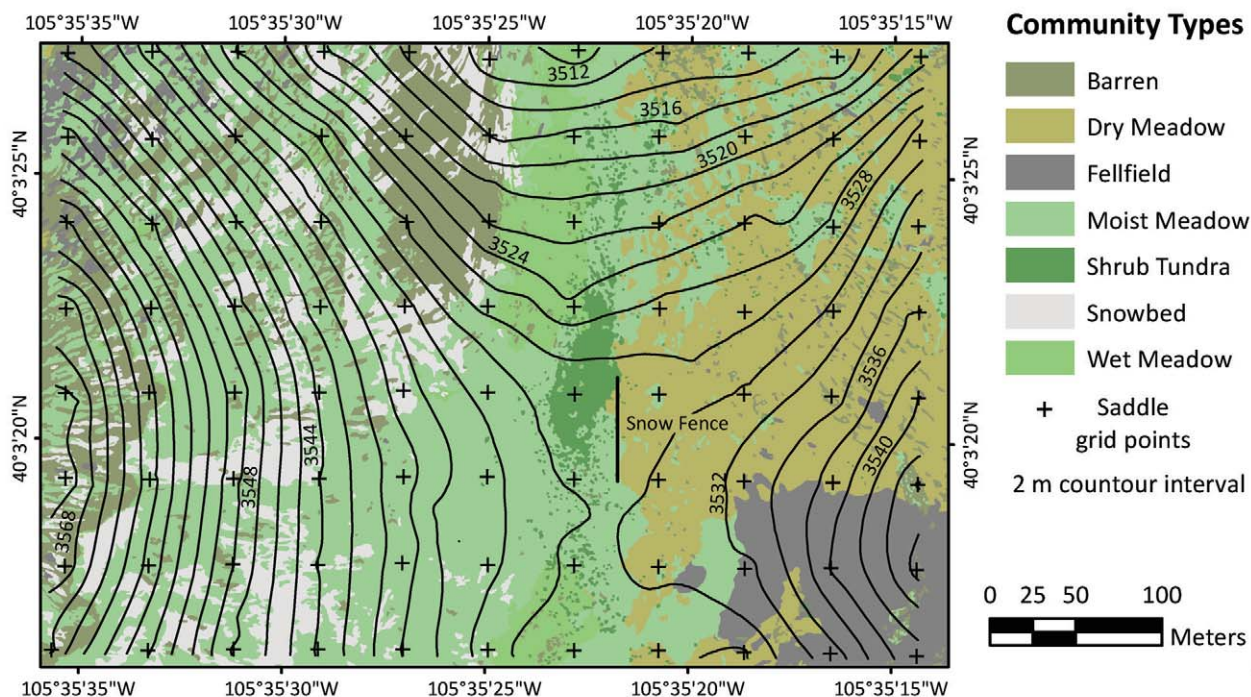


FIGURE 3. Community type map of the Niwot Ridge Saddle based on Walker et al. (1993).

community types. Snow cover on the Saddle has been manipulated since 1994 with a 2.6×60 m snow fence in the center of the saddle grid (Walker et al., 1999). The footprint of the changed snowpack conditions is small compared to the extent of the grid itself, and

since it includes only 1% of the total willow cover in the saddle grid, it does not have a significant effect on the current analysis.

The U.S. Forest Service leased a grazing allotment for sheep encompassing the alpine tundra area on Niwot Ridge from

1940 to 1949, and likely before (Benedict, unpublished data). Sheep grazing has been documented elsewhere in the Colorado Rockies since 1912 (Retzer, 1962). Some cattle grazing also occurred on Niwot, although not to the same extent as sheep grazing (Armstrong et al., 2001). Records during the 1940s from Forest Service range inspectors describe the landscape on Niwot Ridge as being substantially degraded, with few willows (Benedict, unpublished data). Grazing stopped after 1949 (Armstrong et al., 2001).

AERIAL PHOTOGRAPH ANALYSIS

Orthorectified aerial photographs of the entirety of Niwot Ridge were obtained for the following years: 1946, 1953, 1972, 1985, 1990, 1999, 2002, 2004, 2005, 2006, and 2008 (Manley et al., 2009) (<http://culter.colorado.edu/NWT/orthoimagery/orthoimagery.html>). The photographs prior to 2005 are black-and-white and color-infrared and from 2005 on are natural color. They range in resolution from 0.3 to 1 m and were all taken in the spring and summer months (see Table A1 for the specifications of each photograph).

Photographs were analyzed using supervised image classification in ArcGIS 10. In supervised classification, the user manually identifies a subset of pixel regions of known *Salix* cover and regions such as snow beds and fellfield where *Salix* shrubs are known not to be present. The maximum likelihood classification tool then classifies the remaining pixels in the photograph into willow and nonwillow cover according to these user-defined pixel regions (Manley et al., 2009). Supervised image classification was performed on the Saddle area of the most recent 2008 photograph. Pixel regions identified as *Salix* cover were located in the central vein of shrub tundra on the Saddle where ground-based observations from 2012 indicate there is continuous *Salix* cover. Afterward, the classified image was refined by manually removing areas of *Salix* cover where willows were not observed. By this method, the extent of 2008 willow cover was determined. To check its accuracy, the 2008 *Salix* cover classification was compared to the map of Saddle community types identified in Walker et al. (1993). The 2008 *Salix* cover overlapped 71% with the area of shrub tundra in the previous Saddle community map, demonstrating consistency between the two maps.

Performing supervised image classification on low-resolution, black-and-white and color-infrared aerial photographs is challenging because there is less contrast between *Salix* and non-*Salix* pixel values than in color photographs. To lower the chance of classification errors, aerial photographs of Niwot Ridge prior to 2008 were cropped to the extent of 2008 *Salix* cover, reducing the area of analysis to where willow shrubs were known to infill. If *Salix* shrubs were expanding outward over time, the maximum extent of *Salix* cover should occur in 2008; this was verified in a preliminary analysis by performing image classification on the whole Saddle area for photographs prior to 2008. Supervised image classification was then used on these cropped aerial photographs to determine *Salix* cover in each year before 2008. Figure A1 illustrates this cropping and classification process on historical aerial photographs. The full series of aerial photographs cropped to the 2008 extent of *Salix* cover on which supervised classification was performed appears in Figure A2.

Since the time of the season during which the aerial photographs were taken impacts the appearance of shrubs, the specific dates for each photograph are listed in Table A1. The aerial photograph from 2004 was discarded because snow obscured much

of the area in the cropped photograph. The 2008 aerial photograph has a large proportion covered by snow; however, ground-based transect surveys found no willows in any of the snow-covered area.

To determine whether the rate of increase in *Salix* cover on the Saddle is faster in recent decades, both a linear regression and a nonlinear exponential regression were performed in R using function nls (R Core Team, 2012). Model fit was compared with AIC.

SALIX TRANSPLANT EXPERIMENT

A field experiment manipulating winter precipitation, N addition, and summer temperatures in all factorial combinations was initiated in 2006 in moist meadow alpine tundra, approximately 0.75 km from the Saddle grid. The experimental setup is explained in depth in Smith et al. (2012). Briefly, we used a split-plot design in which the whole plot factor is precipitation, and N addition and warming are randomized within precipitation treatment. The experiment consisted of three blocks of sixteen 1-m² plots (48 total plots, 6 replicates for each treatment combination) (Fig. 4). Precipitation was manipulated using snow fences running the length of the center of each block so that the western (windward) eight plots received ambient snow and the

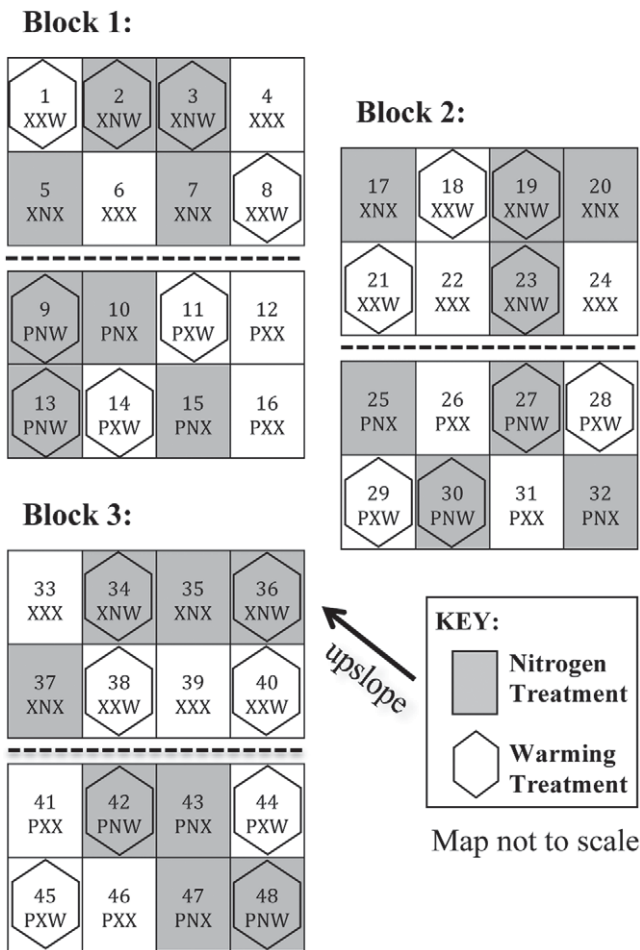


FIGURE 4. *Salix* transplant experiment plot design. Dashed lines represent snow fences. The three letters in each plot indicate treatment combinations. X = control; W = warming treatment; N = nitrogen treatment; and P = phosphorus treatment.

eastern (leeward) eight plots received additional snowpack. On either side of the snow fence, the eight plots were arranged in two rows of four, parallel to the snow fence. Rows of plots on the windward side started 2 m from the snow fence, and rows of plots on the leeward side started 1 m from the snow fence. All plots were separated by 1 m, and plot edges were trenched to a depth of 15 cm to reduce root in-growth from adjacent tundra. Each N and warming treatment combination was replicated twice within each split plot. Nitrogen was added as osmocote slow release fertilizer (urea 40-0-0 N-P-K) at a rate of 28 g N m⁻² yr⁻¹. Growing season temperature was increased by an average of 1 °C using open-topped chambers.

Ten 6-month-old *Salix glauca* seedlings were transplanted into each plot in June 2007 (grown from locally collected seed in a greenhouse). Initial height of each seedling was measured prior to transplanting. In 2012, survival and height of the seedlings were assessed. Seedling survival was assessed by plot. Seedling growth was calculated as the change in height from initial height. The effects of N, temperature, and snow and all two- and three-way interactions on survival and height were analyzed using linear mixed effect models in R, package nlme (Pinheiro et al., 2012). Block was included as a random effect, and the split-plot design was accounted for by modeling snow (within block) as a random effect. Multiple height measurements per plot were accounted for by including plot (within snow and block) as a random effect with compound symmetry error structure.

INVASION DYNAMICS AND VEGETATION ANALYSIS

We analyzed the photograph series to quantify how much willow expansion was due to clonal growth versus dispersed seeds. The ArcGIS Near tool was used to distinguish the origin of willow growth by finding the closest distance between willow polygons from one year to the next. Areas of polygons in a particular year that were directly adjacent (distance equal to 0) to polygons in the previous year were summed to give the area of willow expansion resulting from clonal growth in that year. Areas of polygons with a distance greater than zero were summed to give willow expansion resulting from seed-dispersal.

To assess which community types are being invaded by *Salix*, we used a vegetation map of the ridge from 1987–1988 (Walker et al., 1993). This map contains locations for the seven vegetation types on the saddle: barren, dry meadow, fellfield, moist meadow, shrub tundra, snowbed, and wet meadow. We overlaid the vegetation map with the maps of willow cover derived from aerial photographs from 1990 (approximately when the vegetation map was created) and 2008 (the most recent aerial photograph) and assessed the area of willow cover in each community type. We calculated the change in willow area in each community type, omitting the shrub tundra category since it is defined by willow dominance.

The location and total area of the different tundra vegetation types vary across the Saddle; for example, the main willow vein is surrounded mostly by moist meadow tundra and the large barren and snowbed areas are 50 m away. Thus, we did a second analysis to better assess habitat preference of *Salix*. We first extracted community type data from areas in a 5 m buffer around each of the existing willow patches in 1990 and calculated percentage area of each of the six community types (excluding shrub tundra). Second, looking only at clonal expansion, we assessed the community types where willows expanded from 1990 to 2008. We then calculated preference as percentage of each habitat colonized per percentage habitat availability.

CARBON STORAGE CALCULATIONS

To estimate the effect of *Salix* expansion on the C budget of the alpine tundra, *Salix* area was converted to C biomass. We selected 24 willows of varying sizes in the alpine tundra on Niwot Ridge. The area of each willow was measured, and all aboveground biomass was harvested, dried at 60 °C, and weighed. A linear regression was used to relate aboveground biomass to *Salix* area (mass = $-524.77 + 1039.48 \times \text{area}$, $R^2 = 0.933$, $p < 0.001$), and this equation was used to scale up for the whole Saddle. Belowground and aboveground biomass was harvested from 4 willows, dried and weighed, and the mean aboveground:belowground biomass ratio was found to be 1.54 (± 0.45 SE). This ratio was used to scale up to total (aboveground and belowground) *Salix* biomass on the Saddle. Total C in 8 *Salix* stems was analyzed at the Kiowa Environmental Chemistry Laboratory (Boulder, Colorado, U.S.A.) on a Flash EA 1112 CHN analyzer (CE Elantech, Lakewood, New Jersey), and the average percent C was 49.14% (± 0.55 SE). Conversions from biomass to C concentrations between overstory crowns of Rocky Mountain trees and their roots differ only by a few percent (Jain et al., 2010). Thus we assumed that aboveground and belowground woody biomass has the same percent C and used this to calculate C mass in *Salix* shrubs on the Saddle.

The quantity of C contributed by *Salix* shrubs relative to other alpine tundra plant species on the Saddle was evaluated using aboveground primary productivity from the Saddle from 1992 (available in the Niwot LTER database). We calculated total biomass using a weighted average of aboveground:belowground biomass ratios by community type (Fisk et al., 1998). We measured total C in 42 samples of common forbs (*Acomostylis rossii*, *Artemisia scopulorum*, *Caltha leptosepala*) (43.92%) and 61 samples of common graminoids (*Carex scopulorum*, *Carex rupestris*, *Deschampsia caespitosa*, *Festuca brachyphylla*, *Kobresia myosuroides*, *Luzula spicata*) (44.52%). Percent C for each group was multiplied by the total live forb and graminoid biomass collected in 1992.

Results

Over the 62-year period of study, from 1946 to 2008, willow cover on the Saddle increased 441%, from 427 m² to 2308 m² (0.24% to 1.29% of the Saddle area, Table 1). This increase was exponential ($R^2 = 0.989$, $P < 0.001$, Fig. 5) rather than linear (AIC linear model = 143.7, AIC exponential model = 120.0, smaller AIC indicates better fit), and willows expanded at much higher rates in recent years. As seen from willow cover classification maps developed from aerial photographs in Figure 6 and a selection of aerial photographs of the Saddle paired with larger-scale classification maps in Figure A3, *Salix* shrubs became denser and expanded over time.

The field experiment showed that transplanted willow seedlings had lower survival in the N fertilization treatment ($F_{1,36} = 9.58$, $p = 0.004$) and particularly low survival in the N plus snow treatment after five years (N \times snow interaction, $F_{1,36} = 4.60$, $p = 0.039$, Fig. 7, part a). *Salix* growth was higher with N fertilization ($F_{1,24} = 8.05$, $p = 0.009$) and marginally higher with increased temperature ($F_{1,24} = 2.98$, $p = 0.097$, Fig. 7, part b).

The observed willow growth in the Saddle was mainly due to clonal expansion of existing willows over time (78% of the growth) with a smaller percentage from new patch formation due to colonization by seed (22%). The percentage growth by clonal expansion and seed colonization was constant over time (Fig. 8). The maximum dispersal distance (nearest patch)

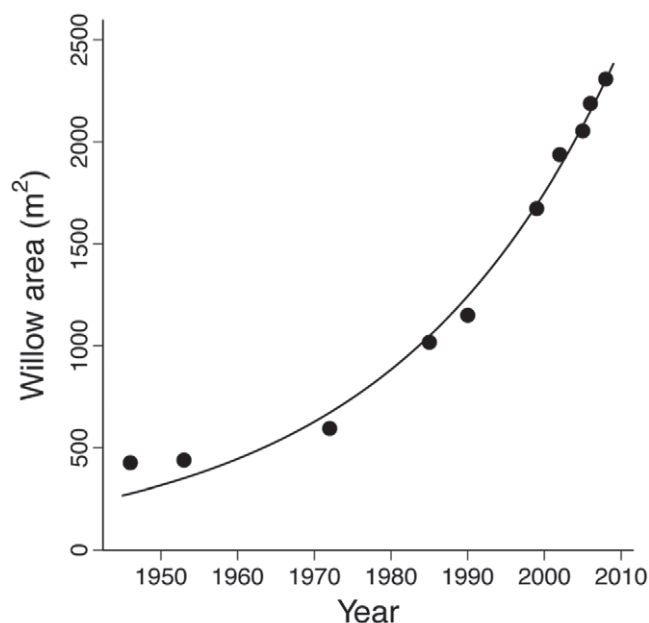


FIGURE 5. Increase in cover of willows on the Saddle, fit with an exponential growth curve ($R^2 = 0.989$, $P < 0.001$).

observed over all the years was 236 m, with a mean dispersal distance of 4.9 m.

By overlaying shrub cover in 1990 and 2008 with a map of community types from 1987–1988, we found that shrubs have the highest rate of invasion into the moist meadow tundra community at $12 \text{ m}^2 \text{ yr}^{-1}$ (Fig. 9, part a), but that shrubs are also invading wet meadow ($4.2 \text{ m}^2 \text{ yr}^{-1}$) and dry meadow ($3.3 \text{ m}^2 \text{ yr}^{-1}$). Very low rates of invasion were found for barren and fellfield communities, and no invasion into snowbed communities was observed. To better assess habitat preference, we weighted clonal growth rates by habitat availability in a 5 m radius around *Salix* shrubs, and we found that *Salix* prefer wet meadow and moist meadow over the other community types (Fig. 9, part b).

TABLE 1
Increases in willow over time at Niwot Ridge.

Year	Percent of 2008 cover	Area (ha)	Percent of Saddle	Carbon storage in Saddle (kg ha^{-1})
1946	18	0.04	0.24	31
1953	19	0.04	0.25	32
1972	26	0.06	0.33	43
1985	44	0.10	0.57	74
1990	50	0.12	0.64	84
1999	73	0.17	0.95	122
2002	84	0.19	1.09	141
2005	89	0.21	1.15	149
2006	95	0.22	1.23	159
2008	100	0.23	1.29	168

The change in shrub cover corresponded to a change in C storage in aboveground and belowground woody biomass from 31 kg ha^{-1} to 168 kg ha^{-1} on the Saddle from 1946 to 2008 (Table 1). Using data from aboveground biomass in the Saddle (Walker, 1997), aboveground:belowground biomass ratios in common tundra community types (Fisk et al., 1998), and mean percent C in common tundra species (this study), we estimate that the total C stored by forb and graminoid tundra vegetation is 3187 kg ha^{-1} . Thus, while *Salix* shrubs only occupy 1.3% of the Saddle area in 2008, they contain 5.0% of the C.

Discussion

Over the past half century, shrubs have increased markedly on Niwot Ridge, expanding by 441%. We found that willows are expanding at increasing rates in recent decades and that willow seedling growth is enhanced by N addition and temperature in the field experiment. Together this suggests that while a release from grazing pressure may explain some of the expansion, global change is likely a contributing factor and that willow expansion will be intensified in the future. We found that willows have a flexible colonization strategy (clonal growth and seed dispersal), which likely contributes to invasion success, and we identified moist meadow communities, and to a lesser extent wet meadow and dry meadow, to be particularly sensitive to invasion. The increase in woody cover on the tundra has implications for C storage, because willows store more C in aboveground and belowground biomass on an aerial basis compared to herbaceous tundra vegetation.

EXPANSION RATES OF SHRUBS

We observed a high rate of increase in shrub cover in our study site from 1946 to 2008: 441% over 62 years, from 0.24% cover to 1.29% cover. This rate of increase is comparable to other studies of shrub invasion in arctic and alpine sites. Another recent study at Niwot Ridge, using three repeat samplings of 1 m^2 plots and transition models, predicted increases in shrub cover of 90%–200% from 1971 to 2071 (Johnson et al., 2011). A study of 19 river valleys in Alaska likewise shows high rates of shrub expansion, especially in areas where shrubs were initially sparse (3%–700% increases in shrub cover over 53 years) (Tape et al., 2006). Three other studies in the Swedish Scandes measured increases in woody plant cover of 56%–87% over 33 years (Rundqvist et al., 2011), 1370% over 98 years (Van Bogaert et al., 2010), and 41% over 13 years (Hedenas et al., 2011). These studies of shrub cover increases are consistent with dendrochronology studies (Hallinger et al., 2010) and count data (Sanz-Elorza et al., 2003), demonstrating increases in individual shrub growth rates and colonization rates in the alpine and arctic.

Because we analyze multiple time points (10) throughout the study period, our study is unique in that we can test whether the rate of shrub expansion changes over time. We find that, in fact, expansion is exponential and accelerating in recent years. This acceleration is consistent with measurements of shrub increase in the alpine Swedish Scandes (Van Bogaert et al., 2010), but interestingly not with the other Niwot Ridge study, which estimates decelerating rates of shrub expansion based on three time point measurements (Johnson et al., 2011). Most studies measuring shrub cover over time have only two time points, so a change in rate cannot be estimated (Sanz-Elorza et al., 2003;

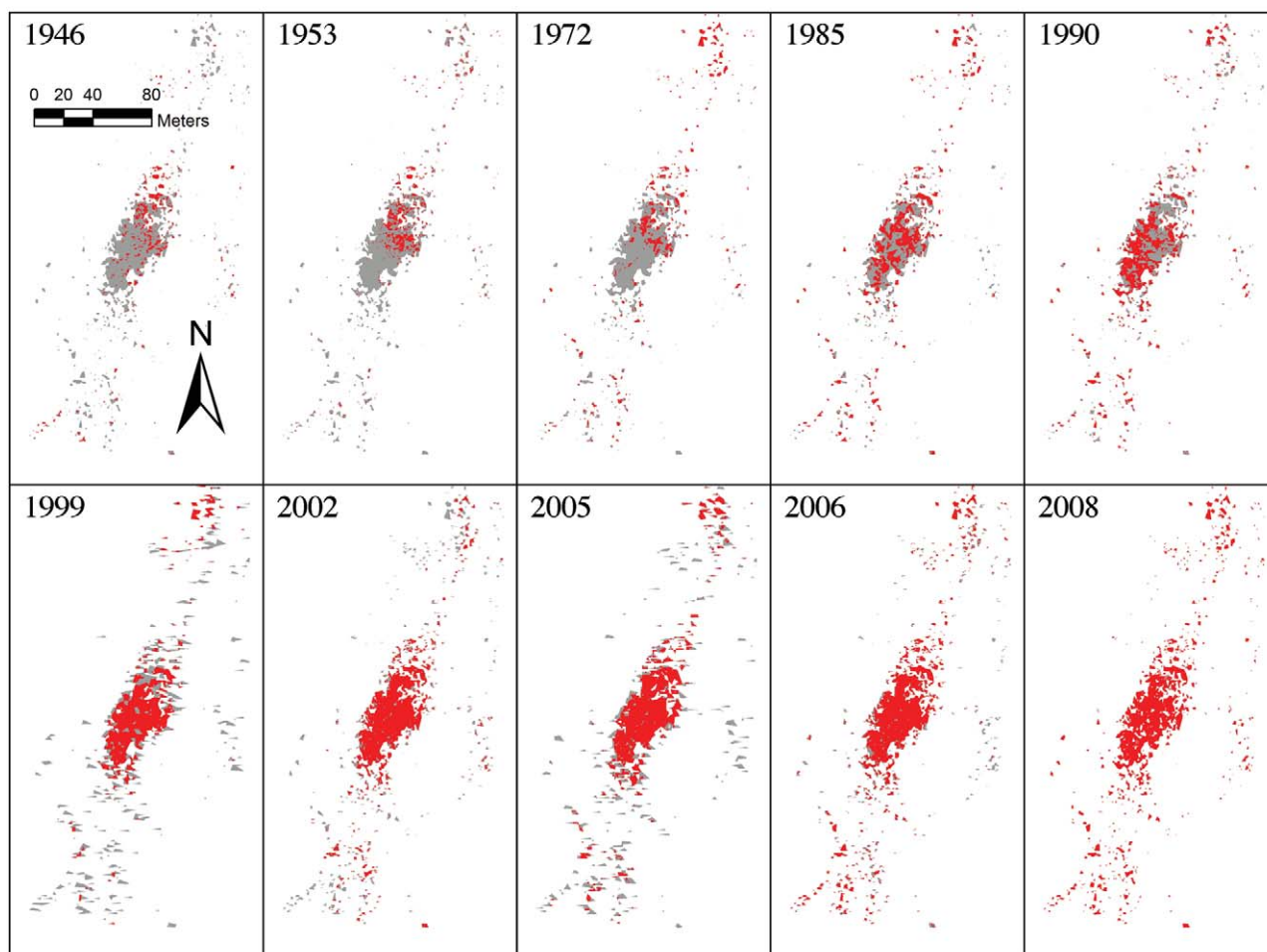


FIGURE 6. Classification maps of *Salix* shrubs on the Niwot Ridge Saddle from 1946 to 2008 over the domain of the maximum extent of shrub cover in 2008. The red represents encroaching shrubs. The gray background image of 2008 shrub cover for each year comprises 1.29% of the study site area or 2308 m².

Tape et al., 2006; Cannone et al., 2007; Hedenas et al., 2011; Rundqvist et al., 2011).

CAUSES OF SHRUB ENCROACHMENT

Global change and land use change often occur simultaneously, which makes identifying drivers of woody

encroachment challenging. We propose that using the expansion dynamics of the invasion may help us infer which drivers are important. In general, long-term enclosure or grazing reduction experiments exhibit linear increases in woody plant cover over time (Chadde and Kay, 1991; Holland et al., 2005; Scherrer and Pickering, 2005). Moreover, responses of shrubs to grazing removal often manifest surprisingly quickly; even in arctic and

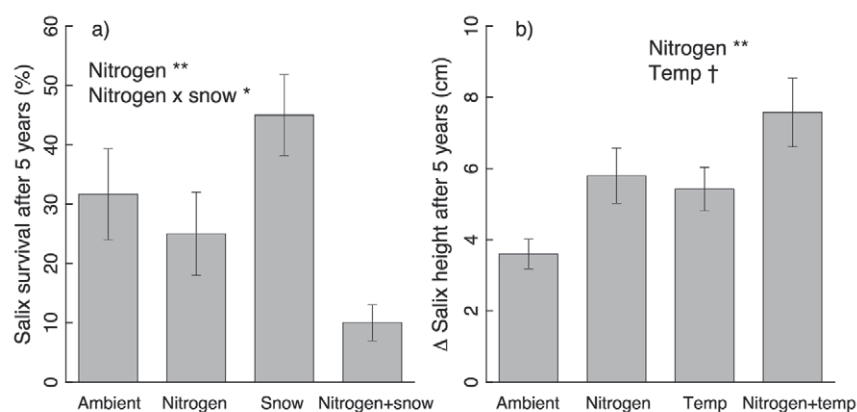


FIGURE 7. *Salix* (a) transplant survival and (b) height after 5 years in the field experiment. Significant effects from ANOVA (including nitrogen, snow, temperature, and all two- and three-way interactions) are presented in each figure († $P < 0.10$, * $P < 0.05$, ** $P < 0.01$). In each figure, treatment means are averaged over nonsignificant treatments.

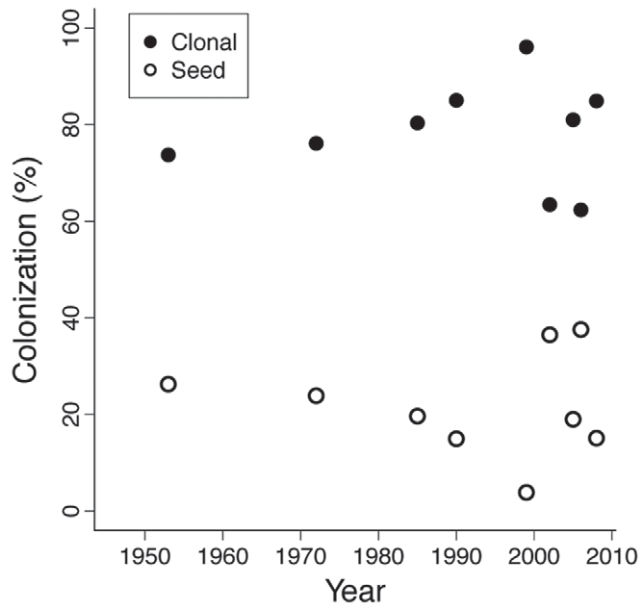


FIGURE 8. Percentage of willow growth from one time period to the next from clonal expansion and colonization by seed (new patch formation).

alpine environments responses are seen within a decade (Olofsson et al., 2009; Hofgaard et al., 2010).

Since 1912, herders have grazed large numbers of sheep during the summers on the tundra in the Colorado Rocky Mountains (Retzer, 1962). Overgrazing caused significant damage to alpine tundra vegetation. In Fraser Experimental Forest, near Niwot Ridge, Retzer (1962) reported that grazing and trails formed by sheep destroyed tundra vegetation and created gullies in the soil

further eroded by wind. At Niwot, sheep were last pastured in 1949; four years after grazing removal (in 1953, our second time point) showed no increase in shrub cover, and 23 years after (in 1972, our third time point) there was only a slight increase. Shrub cover increased more rapidly in the subsequent 36 years of the study period, indicating that the rate of shrub expansion was exponential. Plots in the Saddle are not in exclosures, and it is possible that grazing by elk and other native herbivores, such as bighorn sheep, may have influenced shrub growth dynamics.

Findings of willow expansion at Niwot contrast a general trend of declining willows throughout alpine and subalpine regions of Colorado and Wyoming (Singer et al., 1998; Peinetti et al., 2002; Zeigenfuss et al., 2002, 2011; Kaczynski, 2013). Increased grazing by growing elk populations is likely the main driver of decline (Zeigenfuss et al., 2002), but reduced water availability associated with warmer and drier conditions from climate change and lower water tables and less flooding as a consequence of the loss of beavers may also contribute (Singer et al., 1998). Since the reintroduction of wolves in 1995–1996 in Yellowstone National Park, shrubs have begun to recover, supporting the hypothesis that reduced elk grazing is largely responsible for shrub decline (Ripple and Beschta, 2012). At a high alpine site in Rocky Mountain National Park, declining willow cover coincided with greater elk populations, and in the alpine of the Sangre De Cristo Mountains, willow cover was lower in areas used heavily by elk (Zeigenfuss, 2006; Zeigenfuss et al., 2011). In the area of Niwot Ridge, from 2004–2008, elk populations remained fairly constant, and bighorn sheep were in very low abundance (Colorado Parks and Wildlife, 2004–2008). Together, the exponential increase in shrub cover at Niwot and steady populations of grazers suggest that grazing alone is not driving shrub expansion and that global change drivers likely contribute.

Over the 65 years of the study, winter precipitation has increased steadily, and since the 1980s (when records begin), N deposition has increased at Niwot Ridge. Interestingly, summer temperature exhibited a downward trend from the 1950s to the

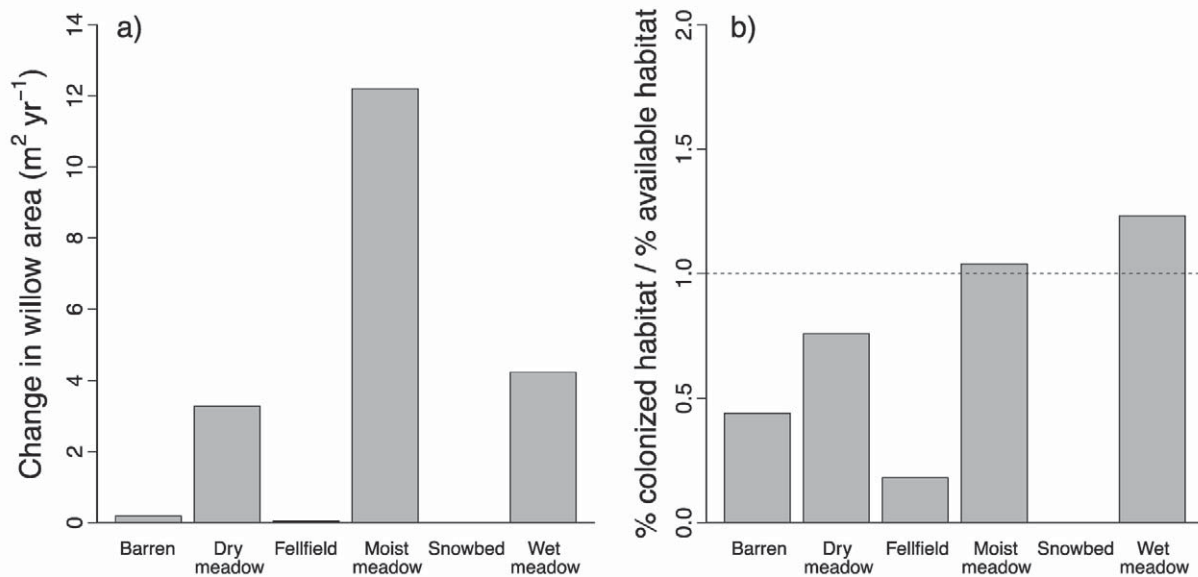


FIGURE 9. Shrub invasion into different tundra community types from 1990 to 2008 by (a) area and (b) ratio of percent colonized habitat to percent available habitat. The percent of clonal expansion into each community type was divided by the percent of each community type in a 5 m radius surrounding existing shrubs in 1990. A ratio greater than 1 indicates that shrubs prefer that habitat (they colonize it at a greater rate than it is available). Note that snowbed communities were a very small percentage of available habitat (0.002%) and no colonization was observed into snowbed areas.

mid-1980s and then increased, exceeding levels at the beginning of the study by the 2000s. Based on other work (Hallinger et al., 2010; Dormann and Woodin, 2002; Sturm et al., 2005b; Elmendorf et al., 2012b), increases in winter precipitation, N deposition, and summer temperature are predicted to have positive effects on shrub growth.

Climate warming has received the most attention as a major driver of the broad-scale arctic and alpine pattern of woody encroachment (Tape et al., 2006). Many studies have correlated increases in alpine and arctic shrub cover and growth with increases in annual and summer temperatures (Cannone et al., 2007; Forbes et al., 2010; Hallinger et al., 2010; Van Bogaert et al., 2010; Johnson et al., 2011). In general, shrubs outcompete tundra vegetation in warming manipulation experiments (Walker et al., 2006) and at lower latitudes in the arctic tundra and lower altitudes in the alpine tundra. In our field experiment, *Salix* seedlings tended to have faster growth rates in warmed plots. Interestingly, in the aerial photograph series, the accelerated increase in shrub cover corresponds to the period when summer temperatures were at an upward trend.

Atmospheric N deposition may be particularly important in augmenting woody encroachment in alpine, rather than arctic, tundra, which receives N inputs from nearby urban areas. N deposition rates at Niwot are reaching critical loads for herbaceous tundra vegetation (Bowman et al., 2006) and thus might trigger changes in woody plant abundance as well. Many nutrient addition experiments in arctic tundra have shown that shrubs, particularly deciduous shrubs, outcompete herbaceous vegetation when fertilized (Chapin et al., 1995; Shaver et al., 2001; Gerdol et al., 2002; Mack et al., 2004), and our field experiment showed that N fertilization greatly increased the growth rate of *Salix* seedlings.

Increased snow depth is hypothesized to promote woody encroachment due to nutrient increases arising from insulation stimulating winter decomposition and nutrient release by soil microbes (Sturm et al., 2005b; Weintraub and Schimel, 2005). Interestingly, we have not observed increases in plant-available soil nutrients in plots with deeper snow depths manipulated with snow fences (Farrer et al., unpublished data) suggesting that the snow-nutrient feedback mechanism may be less strong in alpine tundra, possibly due to high rates of surface flow during thaw. Lack of increased nutrients with deeper snow depths in plots with shrub cover was similarly observed in the alpine in the Yukon Territory in Canada (Myers-Smith and Hik, 2013). Furthermore, the field experiment showed that while snow alone may increase *Salix* seedling survival, snow combined with N fertilization greatly reduced survival. This may be due to strong competitive effects from *Deschampsia cespitosa*, a fast-growing bunchgrass that responds very positively to N (Suding et al., 2008) and snow (Farrer et al., unpublished data). Competitive herbaceous plants may initially limit shrub expansion at the seedling stage, but competitive effects likely decrease as shrubs get larger.

Overall, our experimental results corroborate the interpretation of growth dynamics from the aerial photographs, suggesting that global change contributes to shrub expansion. In fact, it has been shown that the greatest woody plant response occurs when grazing cessation is combined with warming and fertilization treatments (Olofsson et al., 2009). It is likely, then, that the exponential expansion seen in the aerial photographs represents a gradual recovery of woody vegetation from a history of grazing that is intensified by global change in recent decades.

INVASION DYNAMICS AND VEGETATION TYPES AT RISK OF INVASION

Shrubs have two methods of expansion: clonal growth and new patch formation by colonization by dispersed seeds. Not surprisingly, clonal growth comprises the majority of growth from one time period to the next (78%). This is consistent with experimental results that show low rates of seedling survival over five years (28%). The percent of clonal growth versus seed colonization did not change over time; thus, even after 60 years of expansion, willows are still dispersing to new areas creating new patches. This is likely due to the fact that we are still in the early stages of invasion, with willow cover at 1.3% of the Saddle in 2008, and much suitable habitat is still available.

Our study shows that willows are expanding into moist, wet, and dry meadow tundra community types, and they have a slight preference for wetter areas. This is consistent with results from warming experiments that have shown shrubs have a greater increase in cover and height under a mesic (Walker et al., 2006) or mesic to wet moisture regime (Elmendorf et al., 2012a, 2012b). Dry, moist, and wet meadow are very common community types in alpine areas—at our site they make up 66% of the total area of the Saddle—indicating that large areas of the alpine tundra are potentially susceptible to shrub invasion. The long dispersal distances observed here make it clear that willows are not dispersal limited and can easily colonize distant patches of suitable habitat.

CONSEQUENCES OF SHRUB ENCROACHMENT FOR C STORAGE

Shrub expansion will likely significantly alter the alpine tundra C budget. We found that *Salix* shrubs have a greater total (aboveground + belowground) standing C biomass (1296 g C m^{-2}) compared to herbaceous tundra vegetation (323 g C m^{-2}) in the study region. The increase in shrub cover since the 1940s corresponds to an increase in C stored in *Salix* shrubs of 137 kg ha^{-1} . Even though *Salix* only occupies about 1% of the area of the Saddle, it accounts for approximately 5% of the C stored by the herbaceous tundra vegetation covering the remaining 99% of the Saddle area. Because shrubs have higher rates of annual net primary production (ANPP) compared to herbaceous vegetation that is stored in recalcitrant woody biomass, many studies suggest that woody encroachment on the tundra will increase C storage (Hobbie, 1996; Shaver et al., 2001; Bret-Harte et al., 2002; Welker et al., 2004; Knapp et al., 2008). However, the global change factors causing shrub expansion such as warming and N deposition may increase decomposition and C respiration (Hobbie, 1996; Mack et al., 2004; Welker et al., 2004). Positive feedbacks that shrubs initiate, such as increases in snow depth (Sturm et al., 2001), will warm soils and accelerate decomposition. Greater decomposition from global change and snow-shrub interactions may counteract the C sink effect of shrubs. As of yet, it is unclear how these many interacting factors will balance out to affect net ecosystem C storage with climate change; however, our study is a first step in estimating the strength of the woody production component.

IMPLICATIONS AND CONCLUSIONS

Because of the large potential for woody encroachment to alter the physical and biogeochemical processes in the tundra, quantifying shrub expansion rates and understanding the causes and consequences of invasion are critical. Corresponding to patterns in arctic and alpine shrub expansion elsewhere, shrub

cover on Niwot Ridge has shown a marked increase over the past half-century. Analysis of multiple aerial photographs is a powerful method of tracking shrub expansion dynamics over long time scales; the fine-scale resolution that a time series possesses allows us to make conclusions based on spread dynamics. The accelerated rates of expansion seen in recent decades together with the results from a field experiment suggest that global change intensifies the shrub expansion that was likely initiated by the cessation of grazing. We identified three tundra community types at risk of invasion and quantified the importance and extent of clonal and seed-mediated expansion, which is essential for informing management practices. We also estimated that the shrub expansion is associated with an increase in C storage in woody biomass of 137 kg ha⁻¹, which is a first step toward understanding implications of woody encroachment for C balance. Examining the consequences of woody encroachment on wildlife and plant community dynamics is beyond the scope of this paper, but with such rapid increases in cover, there are likely to be cascading effects. For example, willow expansion may facilitate treeline migration because shrubs act as nurse plants for conifer seedlings by moderating local environments (Resler et al., 2005). Willow expansion may also reverse declining trends in ptarmigan populations that rely on willows for habitat and food (Zeigenfuss, 2006). Understanding dynamics of shrub invasion will help to resolve how alpine ecosystems will respond to global change and land-use change and will contribute to better predictive models of shrub expansion.

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APPENDIX

TABLE A1

Aerial photography information.

Year	Resolution (m)	Type	Source date	Source scale
1946	0.3	Black and white	8/31–9/29/46	20,000
1953	0.7	Black and white	9/01/53	46,000
1972	0.8	Color infrared	9/16/72	56,000
1985	0.8	Color infrared	9/06/85	58,000
1990	0.6	Color infrared	8/27/90 and 9/04/88	40,000
1999	1	Black and white	9/06–9/13/99	N/A
2002	0.3	Black and white	Spring 2002	15,000
2005	1	Natural color	7/11–7/13/05	N/A
2006	0.328	Natural color	4–7/06	Digital
2008	0.3	Natural color and color infrared	6/14–6/29/08	Digital

Note: dates given as m/dd/yy, except 2006, which is m/yy.

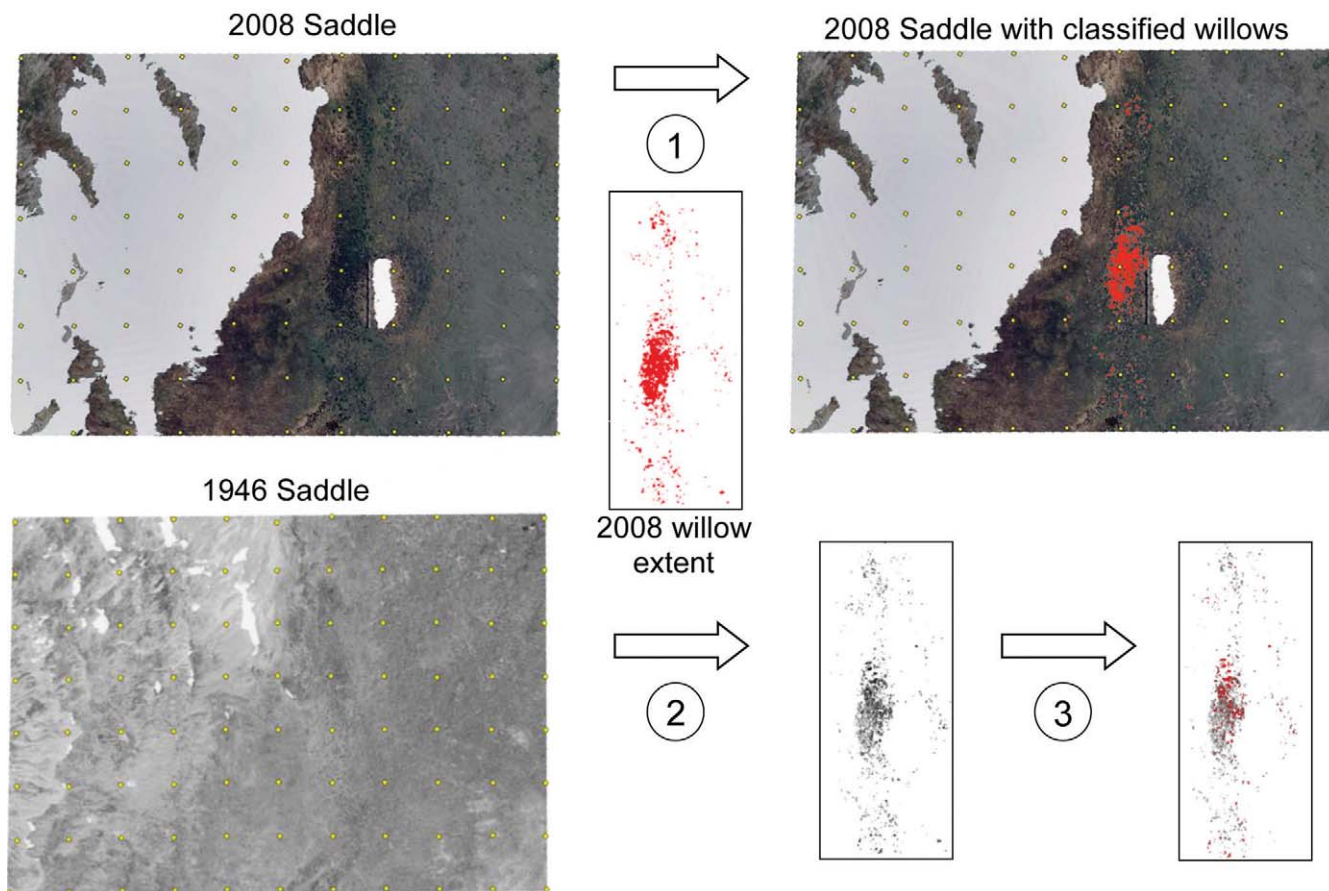


FIGURE A1. Method used for aerial photo analysis: (1) identify willow shrubs in the 2008 saddle aerial photo with supervised image classification; (2) clip previous aerial photo to the extent of 2008 willow cover; (3) identify willows in the clipped previous photo with supervised image classification. Red indicates willow cover. Yellow points indicate Saddle grid points spaced 50 m apart.

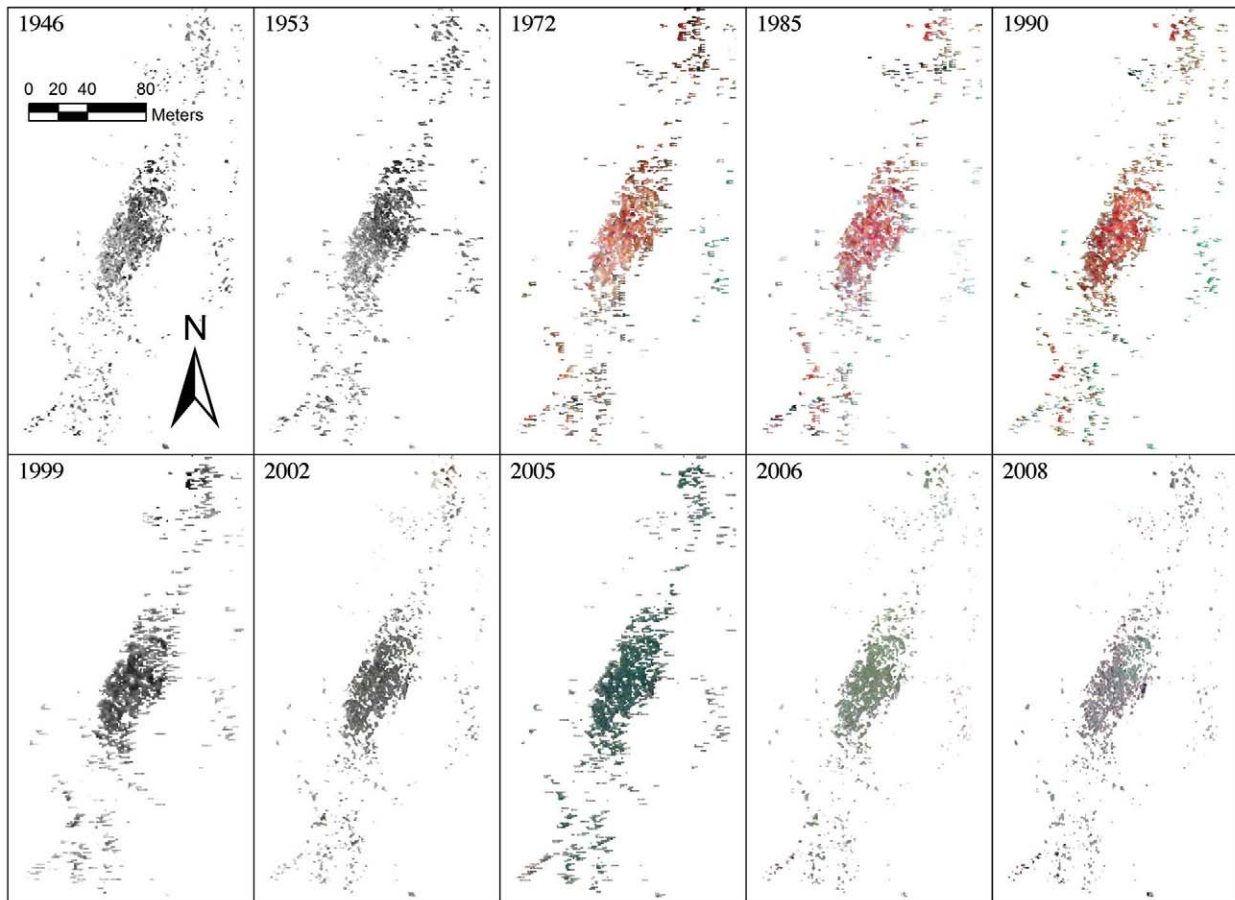


FIGURE A2. Aerial photographs from 1946 to 2008 cropped to the extent of 2008 *Salix* cover. Darker regions in black-and-white and color-infrared photographs were classified as *Salix* cover. Greener regions in color photographs were classified as *Salix* cover.

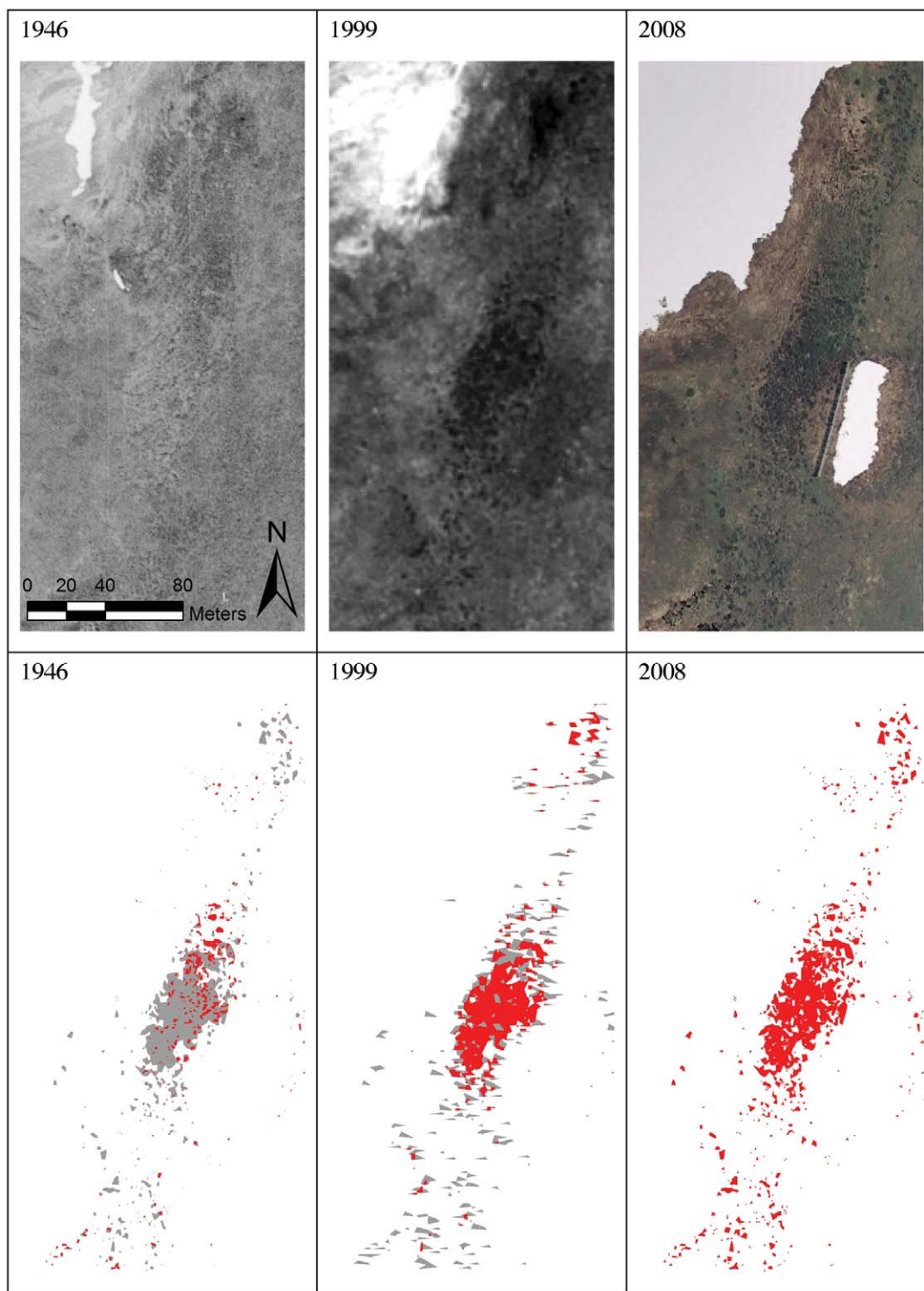


FIGURE A3. Selected aerial photographs of the main Salix vein in the Saddle region and the corresponding Salix cover classifications enlarged from Figure 6. Red indicates Salix cover in the current year, and gray represents the extent of Salix cover in 2008.