Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) Fruit Production in Forest Openings in Banff National Park, Alberta

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Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) is an abundant dwarf shrub in the understory of many areas of subalpine forest in Banff National Park and has the potential to produce fruit important for wildlife. However, the suppression and prevention of wildfires, which began in the early 1900s in the park, have reduced fire-dependent shrubland and open forest and increased the extent of closed, mature forest. Because canopy closure is typically associated with decreased fruit production by understory shrubs, the decline in fire disturbance may be reducing Grouseberry fruit production. To quantify this effect, we measured Grouseberry fruit production under various forest canopies at 10 sites in Banff during 2004–2012. We measured site openness by modeling photosynthetically active direct solar radiation (dPAR) adjusted for overshadowing by topography and coniferous foliage. We found a positive relation between Grouseberry fruit production and dPAR in 2006 and 2010–2012, but not in 2008 or 2009, the 2 years of lowest fruit production; data were lacking for 2004, 2005, and 2007. We also recorded high Grouseberry fruit densities beginning 5 years after fire removed the forest canopy in four prescribed burns conducted during 2001: fruit production was 3.3 to more than 20 times that in adjacent mature forests in 5 of the 6 years analyzed. This study shows the potential ecological benefits of both prescribed burns and wildfire in upper subalpine forests where Grouseberry is widespread, but fruit production is low under the forest canopy.

Key Words: Banff National Park; fruit production; Grouseberry; prescribed burn; photosynthetically active radiation; solar radiation; *Vaccinium scoparium*; wildfire

Introduction

Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) is a dwarf shrub 10–30 cm in height that produces a small, reddish fruit 4–6 mm in diameter (Szczawinski 1962). These fruits are eaten by a variety of birds and mammals (Hamer and Herrero 1987; De Franceschi and Boag 1991; Mattson 1997). Grouseberry is abundant in the understory of many forest communities of Banff National Park, where Grouseberry forest community types cover 28% of a 123-km^2 mapped area in the Front Ranges (Hamer 1985).

Fruit production in many *Vaccinium* species is reduced, sometimes dramatically, under a forest canopy (Hamer and Herrero 1987; Noyce and Coy 1990; Jordano 2000; Greenberg *et al.* 2007). Interception of solar radiation by the forest canopy decreases the amount of photosynthetic energy available to understory plants for production of seed and fruit (Kudo *et al.* 2005). Martin (1983) recorded the production of less than 134 L/ha of Mountain Huckleberry (*V. membranaceum* Douglas ex Torrey) fruit in Montana where canopy cover was greater than 30%; in more open sites, up to 1400 L/ha of fruit were noted. Weaver *et al.* (1990) also found that the abundance of Huckleberry fruit had a strong negative relation to canopy cover ($r^2 = 0.96$). The importance of light was inferred in a Huckleberry study in northwest British Columbia, where fruit production was roughly 50% less in transects where the forest canopy blocked more than 40% of incoming solar radiation compared to transects in sites with greater solar radiation (Burton 1998*).

Before the 20th century, fire was the dominant ecological process affecting forests in Banff National Park. However, since the early 1900s, the incidence of wildfires has declined to a small fraction of the previous rate because of fire prevention and suppression (White 1985). We hypothesized that without wildfires, the extent of post-fire shrubland and open-canopy forest is reduced, causing a decline in Grouseberry fruit production. During 2004–2012, we studied the relation between site openness and Grouseberry fruit production in Banff National Park.

Study Area

Our study area was in the upper subalpine zone of Banff National Park (Figure 1). Annual precipitation was estimated at 50–125 cm (Janz and Storr 1977*). Warm, drying Chinook winds descend the east slopes of the Rocky Mountains and reduce moisture and snow pack, particularly on slopes with a south or west aspect.

Elevations in the park range from 1330 to 3610 m with the treeline at roughly 2300 m. The subalpine zone is at approximately 1500–2350 m. The upper subalpine area, which is generally cooler and wetter, with deeper and longer-lasting snow, begins at roughly 2000 m (Achuff 1982*). Our study sites were at an elevation of 2080–2380 m in the upper subalpine zone where Grouseberry is abundant.
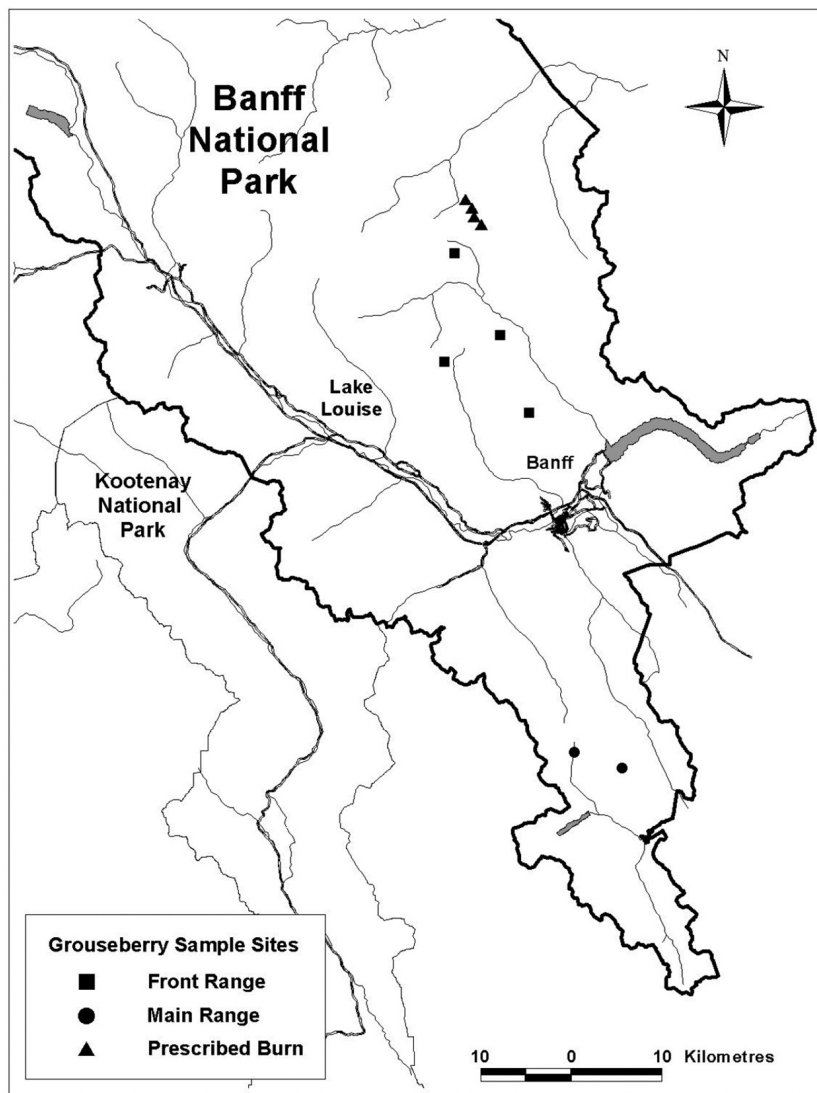
FIGURE 1. Location of Grouseberry study sites in Banff National Park, Alberta, 2004-2012.

The forests in our study area were dominated by Engelmann Spruce (*Picea engelmannii* Parry ex Engelmann). In some sites, Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), Subalpine Fir (*Abies lasiocarpa* [Hooker] Nuttall), and Subalpine Larch (*Larix lyallii* Parlatore) were also abundant. The upper subalpine forest is opened by a variety of factors including fire, avalanches, semi-xeric conditions on exposed southwest-facing slopes, which can lead to grassland and shrubland, and cold air pooling in depressions at the toe of slopes (Hamer 1996).

Because of our sampling design, the understory of most sites was dominated by Grouseberry. Other frequent understory species included Heart-leaved Arnica (*Arnica cordifolia* Hooker), Fireweed (*Epilobium angustifolium* L.), Bracted Lousewort (*Pedicularis bracteosa* Bentham), Pink Mountain Heather (*Phyllodoce empetriformis* [Smith] D. Don), Arctic Willow (*Salix arctica* Pallas), Low Blueberry (*Vaccinium myrtillus* L.), Sitka Valerian (*Valeriana sitchensis* Bongard), and grasses. Regenerating Engelmann Spruce and Subalpine Fir were frequent tall shrubs; willows (*Salix* spp.) occurred in fewer than 10% of the transects.

Methods

Site selection

We established 10 study sites in total: eight in the Front Ranges and two in the Main Ranges (Figure 1). We located one Front Range site in an 1889 burn and a Main Range site in a 1920 burn. These large wildfires had burned into the upper subalpine and created shrubland and regenerating forest with varying degrees of canopy closure, including communities where Grouseberry was a dominant shrub (Hamer and Herrero 1987). Four sites were 6–10 km from the 1889 and 1920 burn sites, where we found relatively accessible terrain, communities with Grouseberry dominant in the shrub layer, and forest openings in stands originating from wildfires that had occurred between 1850 and 1900. Another four sites were located where prescribed burns had been conducted from mid-September through mid-October 2001. These fires removed the forest canopy and scorched the ground layer; *Vaccinium* shrubs had subsequently resprouted from underground rootstocks. The forests in this area were multi-aged, originating from fires that occurred from about 1800 to 1868 (Hamer and Herrero 1987).

Transect selection

We established 11 pairs of transects in the four prescribed burn sites and adjacent forests. Because the fires had run upslope from ignition points, we were able to establish pairs of burned and unburned transects where ignition, rather than habitat characteristics, was responsible for which areas burned.

Transects in the burned areas were at 60–125 m intervals (mean 90 m). Because *Vaccinium* cover was patchy following fire, we adjusted the transect locations by up to a few tens of metres from the systematically located points to ensure relatively high *Vaccinium* cover (mean 41%, standard deviation [SD] 18%). We located control transects in the unburned adjacent forest along the same elevational contour as the burned transects, with similar adjustment to locate transects in communities where *Vaccinium* was dominant in the shrub layer (mean 62%, SD 16%). We established five transect pairs in the largest burn, two pairs in a burn 1.2 km north, and two pairs in a burn 1.1 km south of the largest burn, all on westerly slopes of 215–271°. Two pairs of transects were located in a fourth burn, on an easterly slope of 84–124°.

The six additional sites in the study area were also established where *Vaccinium* was dominant in the shrub layer (mean cover 57%, SD 15%). At each site, we located one or more transects under a forest canopy cover of less than 40%. When the terrain and Grouseberry cover were suitable, we established transects with notably different slope aspects and forest cover.

Transect analysis

The ends of each transect were marked with permanent metal bars. We recorded transect location and elevation using a handheld geographic positioning system unit and slope steepness and aspect using a compass with built-in clinometer. In the year when transects were established, we estimated *Vaccinium* cover and height at 1-m intervals on the 20-m transects (i.e., 20 measurements/transect). We estimated cover visually to the nearest 5% using a 10 cm by 10 cm frame and measured height as the length of the longest *Vaccinium* shoot rooted within 5 cm of the *Vaccinium* stem rooted nearest to a preselected corner of the frame.

We estimated Grouseberry fruit density by counting all fruits within a 20 cm by 20 cm frame placed at 2–m intervals along the 20–m transect (10 quadrats/transect). At each 2–m point, a 180° forward-facing selection zone (Hamer 1996) was scanned and the frame was placed in the first available location with more than 70% *Vaccinium* cover (lower cover was accepted if the alternative meant moving the frame more than 2 m from the original 2-m point). Because of these subjective criteria, quadrats were not in exactly the same location each year. Fruits were picked to ensure that each was counted only once. *Vaccinium* cover in the quadrat was estimated to the nearest 5%. Counts were then scaled to 100% *Vaccinium* cover (e.g., a quadrat with 35 fruits and 50% *Vaccinium* cover scored 70 fruits) to allow comparison among locations with varying *Vaccinium* cover. In other words, we calculated fruits/m² of *Vaccinium* shrub cover, not fruits/m² of habitat. Because fewer than 1% of the fruits we counted in 2004–2012 were Low Blueberry, we refer to fruits as Grouseberry. Because Grouseberry and Low Blueberry can be difficult to separate based on vegetative characteristics (Szczawinski 1962, Vander Kloet and Dickinson 1999), we report cover and height for *Vaccinium* species.

Estimating solar radiation

Although forest canopy is a primary cause of shading, nearby or tall mountains also block solar radiation. Thus, we measured site openness by modeling direct photosynthetically active radiation (dPAR) adjusted for overshadowing by both topography and coniferous canopy.

We calculated the relative amount of dPAR (band 1, wavelength 290–700 nm) received at our transects under cloudless conditions by applying the REST2 model (Gueymard 2008; Gueymard and Myers 2008), using site-specific latitude, slope aspect, slope steepness, and elevation. We calculated radiation at 1-minute intervals from sunrise to sunset and summed these values for 1 June to 31 August. We chose this 92-day period because we did not have an a priori prediction of the critical time for Grouseberry flower and fruit development and because the length of the growing season varies from year to year depending on weather and snow melt and among sites depending on microclimate.

We imposed an overshadowing function that set dPAR to zero when the height of obstacles on the solar azimuth blocked the sun by exceeding the solar altitude (Quaschning and Hanitsch 1998; Yard *et al.* 2005).

We used a clinometer (Suunto, Vantaa, Finland) and a Ranger sighting compass (Silva, Bromma, Sweden) to record the height (degrees of elevation above horizon) and horizontal sweep (compass bearings) of obstacles, whether geological features or fully closed canopy of coniferous foliage, for azimuths 50° through 310° (i.e., sunrise to sunset at the summer solstice). We recorded these data for each relatively homogeneous block of foliage or terrain; blocks ranged from 1° to several tens of degrees of horizontal sweep (block average 7.2°).

We imposed a second overshadowing function on the model to partly restrict dPAR because of the partial shade resulting from open coniferous canopy. We recorded the angular height and horizontal sweep, plus the average canopy openness in 5% increments from 5% for essentially closed canopy (sky almost completely obstructed; 5% of dPAR transmitted) to 95% for essentially no foliage (sky almost fully visible; 95% of dPAR transmitted), for each relatively homogeneous block of coniferous foliage (block average 18.2°), from azimuths 50° through 310°. Because these readings required subjective estimation of coniferous canopy density, all data were recorded by the same observer to avoid inter-observer variability.

These two procedures for estimating overshadowing often captured coniferous foliage up to 200 m away and, hence, were not equivalent to the "fish-eye" lens photographic method often employed in forest-gap studies (e.g., Englund *et al.* 2000).

We calculated dPAR at the 7-m and 13-m marks on our 20-m transects and averaged these to obtain one value per transect. Because comparisons among transects were relative in our analyses, we did not require absolute PAR values. Thus, we did not require continuous integration over the entire day, nor did we require locally corrected values for atmospheric parameters used by REST2 (we used REST2 default values).

We calculated only direct radiation (roughly 77–81% of total PAR, calculated for our transects using REST2 without overshadowing). Indirect PAR radiates from the entire sky, but not isotropically. Complex modeling of overshadowed, indirect, anisotropic PAR (Gueymard 1987) was beyond the scope of this study, as was measurement of the relatively minor shade created by shrubs and herbs.

Data analysis

Because of logistics associated with our remote sites, not all transects were established until 2009, and not all transects were monitored annually. In addition, we excluded 2007 data from our analyses, because that year many grouseberries on warm, south and west aspects ripened early and then became desiccated. When we began our counts, many fruits at warm sites had fallen, and other fruits fell to the ground when we touched the shrubs, becoming unrecognizable in the litter.

We scaled dPAR values relative to that from the transect with the largest dPAR value, which was set at 100.

To avoid pseudoreplication, we combined the 22 transects at the prescribed burn sites into eight sampling units, i.e., the four burn sites and the four adjacent unburned forests, and we combined three transects at another site because they had essentially the same slope steepness, aspect, and forest cover. This produced 15–39 sampling units (transects or collapsed transects) for 2006–2012. Because the transects at the prescribed burn sites were reduced to four pairs of sampling units, we present differences in fruit densities between burned and unburned habitat using descriptive statistics.

Fruit densities were characterized by large variability, with numerous outliers. Therefore, we used robust regression analysis (R open-source software, version 3.0.2, WRS package) to assess the relation between fruit production and dPAR. This robust Theil-Sen based regression method uses bootstrap to analyze unconventionally distributed data and more accurately reflects trends in the data compared with ordinary least squares methods or nonparametric data transformations, which can give biased results (Wright and Field 2009).

Results

Annual fruit abundance

Based on 28 sampling units for which we had continuous records during 2008–2012, and scaling results relative to the year of highest fruit density (2010), we recorded relative Grouseberry fruit abundance of 22% in 2008, 35% in 2009, 100% (reference year) in 2010, 32% in 2011, and 48% in 2012. We also estimated relative abundance of 103% in 2006 based on 15 sampling units for which we had continuous records for 2006–2012.

Prescribed burns

In 2004, 3 years post-fire, Grouseberry fruit density in the burned transects averaged 0.17 times that in the adjacent, forested transects at the two sites we measured (Figure 2). The 2001 fires had burned the Grouseberry plants to ground level, and the plants were immature in 2004 (average Grouseberry height in the burns, 5.6 cm
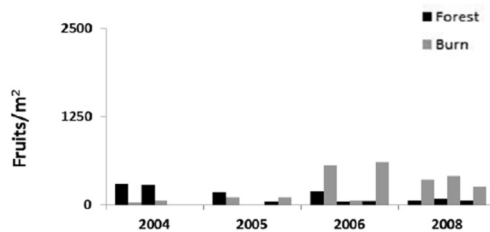

Figure 2. Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m² of *Vaccinium* cover) during 2004–2008 at three prescribed burns conducted in Banff National Park, Alberta, during autumn 2001. Matched transects were located in adjacent, unburned forests. Data are missing for the third burn in 2004, the second burn in 2005, and all burns in 2007 when early fruit-fall invalidated counts.

[SD 0.9 cm] versus 12.7 cm [SD 1.9 cm] in the forests). In 2005, 4 years post-fire, results were mixed: one burn had 0.64 times the fruit density of the forested transects, whereas the second burn we measured had 2.3 times the fruit density of the forested transects.

In 2006 and 2008, 5 and 7 years post-fire, fruit densities in the three burns averaged 5.7 times and 4.8 times the densities recorded for the forested transects, respectively. There are no data for 2007, when early fruit-fall invalidated our counts.

In 2009, 8 years post-fire, fruit densities in the three west-facing burns averaged 0.41 times those in the forested transects, but at the east-facing site, fruit density in the burned transects was 10.1 times that in the adjacent, forested transects (Figure 3). During 2010–2012, fruit densities in the three west-facing burned transects were 3.3 times to more than 30 times those in the adjacent forested transects; those in the east-facing burned transects were 6.2 to more than 20 times those in the forested transects. Not all ratios are defined because the scarcity of fruits in some forested transects resulted in very small denominators and, thus, misleading ratios.

Relation between Grouseberry fruit density and site openness

Grouseberry fruit densities were positively associated with dPAR in 2006 and 2010–2012 ($P < 0.02$), but not in 2008 or 2009 ($P > 0.35$, Table 1). In 2010–2012, this positive relationship held whether the four sampling units in the prescribed burns were included or excluded ($P < 0.02$, Table 1). Figure 4 illustrates results for 2010, the year of highest fruit density.
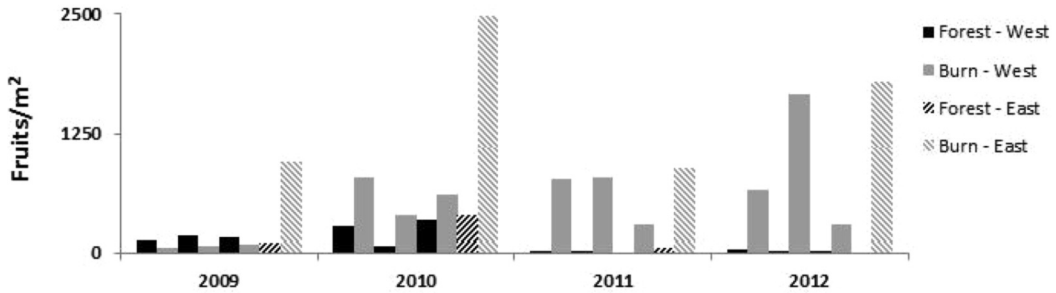

FIGURE 3. Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m² of *Vaccinium* cover) during 2009–2012 at three west-facing prescribed burns and one east-facing prescribed burn conducted in Banff National Park, Alberta, during autumn 2001. Matched transects were located in adjacent, unburned forests.

TABLE 1. Association between Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production and incoming direct photosynthetically active radiation including and excluding the four prescribed burn sites, Banff National Park, Alberta, 2006–2012.

| Year	Intercept	Regression coefficient b (95% CI)	Explanatory power	n	P
Including prescribed burns					
2006	−412	11.25 (0.39 to 25.16)	0.45	15	0.017
2008	50	0.03 (−0.57 to 2.04)	0.00	34	0.354
2009	142	−0.65 (−2.37 to 2.42)	0.04	33	0.993
2010	−51	7.70 (4.65 to 14.04)	0.38	37	< 0.001
2011	−172	3.50 (0.33 to 8.29)	0.47	34	< 0.001
2012	−195	4.72 (2.16 to 9.01)	0.49	34	< 0.001
Excluding prescribed burns					
2006	579	14.93 (−7.72 to 15.72)	0.38	10	0.541
2008	61	−0.34 (−1.84 to 0.756)	0.05	27	0.514
2009	153	−0.90 (−4.18 to 1.83)	0.04	28	0.541
2010	30	5.84 (2.51 to 12.99)	0.21	31	< 0.001
2011	−52	1.24 (0.15 to 5.69)	0.21	28	0.015
2012	−114	3.16 (1.09 to 6.54)	0.34	28	0.007

Note: CI = confidence interval.
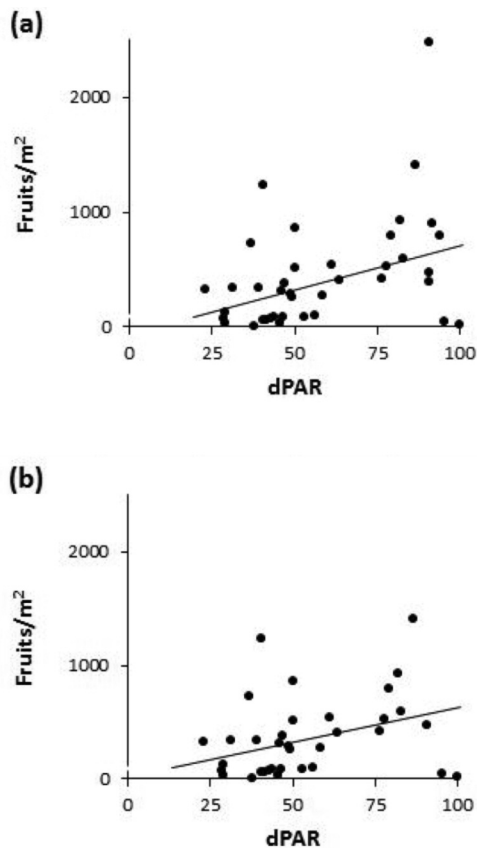
FIGURE 4. Relation between Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m² of *Vaccinium* cover) in 2010 and direct photosynthetically active radiation adjusted for overshadowing by topography and conifer foliage and summed for the 92-day period from 1 June through 31 August in Banff National Park, Alberta, including the four prescribed burns (a) and excluding the four prescribed burns (b). The best-fit lines were derived from Theil-Sen robust regression.

Discussion

We recorded high Grouseberry fruit densities in the open sites created when the 2001 prescribed fires removed the forest canopy. During 2006–2012, fruit densities at the burn sites were 3.3 to more than 30 times those in the adjacent forest except in 2009 when density was high only in the east-facing burn site (Figures 2, 3). Similarly, Weaver *et al.* (1990) reported that Grouseberry fruit production at a site where the Whitebark Pine (*Pinus albicaulis* Engelmann) canopy had been removed was 6 times that in two adjacent forests. High fruit production at sites where fire, logging, avalanching, or other factors have removed the forest overstory is common for many fruiting species (Lindzey *et al.* 1986; Hamer 1996; Greenberg *et al.* 2007; McCord *et al.* 2014).

We attribute the fact that, 3 and 4 years following fire, fruit production was lower in the west-facing prescribed burns than the adjacent forests in three of the four cases (Figure 2) to the time required for Grouseberry shrubs to re-establish following fire. The fires removed the above-ground portions of the Grouseberry shrubs and left a black scorched surface layer. Five years post-fire, however, the burned transects produced 5.7 times more fruits than the transects in the adjacent forests. A Buffaloberry (*Shepherdia canadensis* [L] Nuttall) study in the same valley of Banff National Park also found a 5-year lag in fruit production following prescribed fire (Hamer 1996).

Changes in soil nutrient status can occur following fire. However, in our prescribed burns, by 2012 (11 years post-fire), the fires' effects on nutrient cycling may have been minimal. The effect on nutrients can be greatest immediately following fire, but nitrogen can return to pre-fire levels in a few years and phosphorus in a few months; effects on other nutrients can be even more ephemeral (Certini 2005). We did not conduct soil or nutrient analyses for our study area.

We found a positive relation between Grouseberry fruit density and dPAR in 4 of the 6 years analyzed (Table 1). There was no significant relation in the 2 years of lowest fruit production. For 2010–2012, these positive relations held, with or without the prescribed burn sites included in the analysis, and, hence, were not simply driven by the higher fruit production we found in the prescribed burns following the 5-year lag in post-fire recovery. In 2006, the relation between dPAR and fruit density did not hold when the burns were excluded, but this analysis is based on only 10 sampling units because several study sites had not yet been established.

When measuring fruit density, we subjectively repositioned our quadrats (normally by a few decimetres or less) from the 2-m marks along transects when necessary to ensure high cover of *Vaccinium* inside the frame. We also converted these counts to a 100% *Vaccinium* cover basis to standardize fruit densities among sites and observers. Thus we measured relative or ecological fruit density per square metre of *Vaccinium* cover, not absolute fruit density per hectare of habitat. This approach emulates the behaviour of frugivores, which can forage with high efficiency by moving from shrub to shrub (patch to patch).

Although we recorded high fruit densities at the four burn sites we studied, we searched seven other prescribed burns in Banff National Park, but did not find sufficient *Vaccinium* cover for sampling. These other burns were typically in warmer habitat at lower elevations where there was a high cover of grasses and other herbs. We also recorded low Grouseberry fruit densities in some open but xeric, south-facing habitat. This included an open, xeric, south southwest-facing transect with the highest dPAR value of our study. During 2008–2012, this transect averaged 0.29 times the fruit density of a second transect located 20 m away

under more mesic conditions associated with 40% forest canopy cover. Keefer *et al.* (2010*) reviewed studies on Huckleberry that similarly found reduced fruit production in fully open sites. We also recorded fruit densities that were 5 or more times and 3 or more times higher in the more mesic east-facing prescribed burn site than in west-facing burn sites in 2009 and 2010, and equal or greater densities in 2011 and 2012 (Figure 3). Although this observation is based on only one east-facing burn site, it is consistent with observations from Huckleberry studies. For example, Martin (1983) found that the most productive Huckleberry sites were in north- and east-facing burn sites. Similarly, the highest fruit densities recorded in a Buffaloberry study in Banff National Park were on north northeast-aspect slopes (Hamer 1996). A positive influence of mesic site conditions on fruit production was also suggested by Burton (1998*), who reported a stronger relation between Huckleberry fruit production and site moisture conditions, than between fruit production and solar radiation.

Our study did not specifically address the effects of mesic site conditions given that it was limited in extent (to 39 or fewer sampling units), focused on dPAR, and did not permit a more comprehensive multivariate analysis. Nevertheless, we have shown that Grouseberry fruit production increases with increasing site openness and that moderate to high fruit production can be restored when prescribed fire is applied in appropriate habitat types.

Many of the prescribed fires in Banff National Park have been on warmer slopes (e.g., south and west aspect) and more often in the lower subalpine than in the upper subalpine or near the treeline. When prescribed fire is used on these warmer, drier slopes, the post-fire community is often dominated by grasses. In contrast, historic wildfires that burned through mesic, upper subalpine habitat near the treeline have, in some cases, led to extensive, open Grouseberry communities. Our study documents the ecological benefits of both high-elevation prescribed burns and wildfire in forests where Grouseberry shrubs are widespread but fruit production is low under the forest canopy.

Acknowledgements

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