

Effects of spruce beetle infestations on berry productivity on the Kenai Peninsula, Alaska

Lowell H. Suring^a, Michael I. Goldstein^{b,*}, Susan Howell^{c,1}, Christopher S. Nations^d

^a U.S. Forest Service, Terrestrial Wildlife Ecology Unit, Forestry Sciences Laboratory, 22 East Front Street, Boise, ID 83702, USA

^b U.S. Forest Service, Alaska Regional Office, P.O. Box 21628, Juneau, AK 99802, USA

^c U.S. Forest Service, Seward Ranger District, Chugach National Forest, Seward, AK 99664, USA

^d Western EcoSystems Technology, 2003 Central Avenue, Cheyenne, WY 82001, USA

Abstract

Understanding the dynamics of berry productivity provides significant insight for managing the landscape to maintain ecosystem functions. On the Kenai Peninsula, as many as 14 mammal and 30 bird species commonly feed on berries produced by shrubs and forbs associated with spruce forests. Brown bears (*Ursus arctos*) and black bears (*Ursus americanus*), in particular, rely on berry crops for foraging. Gathering berries for subsistence or recreation purposes is also important to local residents and visitors. Recent spruce beetle (*Dendroctonus rufipennis* Kirby) infestations on the Kenai Peninsula have altered the dynamics of berry productivity. To assess this relationship, we evaluated the number and productivity of berries with the following environmental covariates: canopy cover, overstory type, infestation level, year of infestation, land type, and land type association. Data were sufficient to describe the relationships of these variables with the productivity of bunchberry dogwood (*Cornus canadensis*), black crowberry (*Empetrum nigrum*), false toadflax (*Geocaulon lividum*), strawberryleaf raspberry (*Rubus pedatus*), lingonberry (*Vaccinium vitis-idaea*), and a combination of 24 other species. We accomplished this using log-linear regression by which we estimated the variance using the negative binomial distribution. Canopy cover significantly influenced the productivity of all berry species except for false toadflax. Increasing canopy cover had a negative effect on berry productivity except for strawberryleaf raspberry. Overstory type influenced the productivity of all individual berry species. Infestation level was significantly related to the productivity of black crowberry, false toadflax, and the combined species group. Berry counts were generally lower in plots with low or medium infestation than in plots with high infestation. Relating the dynamics of berry productivity to the effects of spruce beetle infestations provides the opportunity for better management of post-beetle-infested forests.

© 2006 Published by Elsevier B.V.

Keywords: Alaska; Berry; *Dendroctonus rufipennis*; Kenai Peninsula; Spruce beetle

1. Introduction

The spruce beetle infestation through the 1990s altered the landscape of the 2.33 million ha Kenai Peninsula, Alaska (Holsten et al., 1995a). The recent epidemic infested nearly 0.5 million of the 0.8 million forested ha (Reynolds and Holsten, 1996; Wittwer, 2004) and likely led to changes in the distribution and productivity of berry-producing plants. Understanding the dynamics of berry productivity as related to the effects of the spruce beetle infestation provided insight into opportunities for managing the landscape for wildlife species that rely on

berries as a major portion of their seasonal diet and for people that utilize berries for subsistence or recreation purposes.

The Kenai Peninsula ecosystem supports a diverse assemblage of wildlife (131 species), including 8 endemic subspecies (L. Suring, U.S. Forest Service, unpublished data). Populations of nearly 77% of these species have or will be affected by changes in habitat resulting from the disturbances associated with the spruce beetle infestation (Suring, 1998). On the Kenai Peninsula as many as 14 species of mammals and 30 species of birds commonly feed on berries (Martin et al., 1951; Erhlich et al., 1988). The spruce beetle infestation changed the forest canopy structure and directly affected habitat use by many forest birds (Lance and Howell, 2000; Matsuoka et al., 2001). Changes in understory vegetation as a result of decreased overstory competition affected habitat used by small mammals (Williams, 1999; Matsuoka et al., 2001; Lance et al., 2006). Similarly, changes in browse availability altered how

* Corresponding author. Tel.: +1 907 586 7905; fax: +1 907 586 7877.

E-mail address: Goldstein.mi@gmail.com (M.I. Goldstein).

¹ Present address: U.S. Forest Service, Tongass National Forest, Thorne Bay Ranger District, P.O. Box 19001, Thorne Bay, AK 99919, USA.

moose used this landscape (Collins and Schwartz, 1998). Brown and black bears relied on berry crops for foraging during summer and fall (Risdaal, 1984; Smith, 1984; Schwartz and Franzmann, 1991). In this paper, we evaluated the extent that changes in forest structure resulting from spruce beetle infestation affected berry production. Specifically, we quantified the number and mass of berries and their relationship to stand and landscape characteristics. This information provided an improved understanding of the effects of spruce beetle infestations on berry productivity and subsequent conservation and management of post-infestation forests.

2. Methods

2.1. Study area

We chose a study area within the Chugach National Forest on the Kenai Peninsula, Alaska, from Portage south to Seward and west to the boundary of the Kenai National Wildlife Refuge, an area of nearly 500,000 ha. The topography of the study area consisted of rounded to jagged mountains separated by alpine, glacier-shaped valleys. Elevations ranged from 30 to 1800 m. The marine and arctic–continental climate on the Peninsula is wet and transitional with mild to cool summers and cool winters. Mean annual temperatures varied from 4 to 7 °C and annual precipitation varied from 50 to 200 cm. Conifer forests in the area included white spruce (*Picea glauca*), Lutz spruce (*Picea × lutzii* [*glauca* × *mariana*]), mountain hemlock (*Tsuga mertensiana*), and black spruce (*P. mariana*). Mountain hemlock occurred primarily on side slopes at low to mid-elevations while the spruces dominated on both valley bottoms and side slopes. Paper birch (*Betula papyrifera*) was a major component of mixed conifer–deciduous forests. Deciduous forests of black cottonwood (*Populus trichocarpa*) and willow (*Salix* spp.) were normally found in the valley bottoms. Common understory species included bluejoint (*Calamagrostis canadensis*), rusty menziesia (*Menziesia ferruginea*), oval-leaf blueberry (*Vaccinium ovalifolium*), devilsclub (*Oplopanax horridus*), lingonberry, and black crowberry. DeVelice et al. (1999) documented 32 species of berry-producing shrubs and forbs on the study area, of which 20 occur commonly. The study area was located within the Chugach–St. Elias Mountains (Nowacki et al., 2001).

2.2. Sampling sites and sample size

We sampled vegetation among land type associations (a landscape unit formed and influenced by similar geomorphic processes) and land types (a landscape unit with more detail than land type association having one major geomorphic process, one major landform, and a complex of soils and plant communities) that were previously described (Davidson and DeVelice, 2001). Land type associations included mountain slopes, hills, and lowlands. Land types included frequently dissected, deeply incised mountain slopes; frequently dissected, shallowly incised mountain slopes; forested lower side slopes; non-forested lower side

slopes; alluvial fans; braided rivers; marine terraces; high relief terraces; low relief hills; and high relief hills. We sampled forested stands within these areas that were potentially infested by spruce beetles.

We established a grid across the study area with 400 m × 400 m cells using a geographic information system. Grid intersections falling in stands dominated by spruce or mountain hemlock with a spruce component provided 339 potential starting points for line transects. We established 96 transects (46 in 1999 and 50 in 2000) from randomly selected starting points. We established a line transect with random direction at each starting point, set up the first sample plot on each transect randomly between 1 and 20 m from the initiation point, and established nine additional sample plots at 20-m intervals along the transect.

2.3. Data collection

We used a rectangular frame encompassing 1 m² to define the sample plots (Cherkasov, 1974; Smith, 1984). At each sample plot we visually estimated, and recorded as a cover class (i.e., 0–5, 6–15, 16–25, 26–35, 36–45, 46–55, 56–65, 66–75, 76–95, and 96–100%), the proportion of the plot covered by each berry-producing species, proportion of other vegetation, and proportion of non-vegetation. All cover in a plot summed to 100%. We recorded an oblique image of each plot with a digital camera. We also used the digital camera to record an image of the overstory canopy cover at each sample plot using a 37 mm wide-angle lens at a standard height, similar to the method of Kirchoff and Thomson (1998). We measured canopy cover using the proportion of “covered” pixels in the digital image. We estimated the proportion of beetle-infested white and Lutz spruce trees within 10 m of the sample plot as low (1–10%), medium (11–40%), or high (>40%) compared to all white/Lutz spruce present ≥15 cm diameter at breast height. Initial year of infestation of trees by spruce beetles, taken from digital survey data compiled by Alaska Department of Natural Resources, was assigned to each sample plot.

We counted all berries within the sample plot by species and described their phenology (i.e., flowers, green fruits, ripe fruits, and empty fruiting stalks). During the peak of the fruiting season for each species, we collected 10 ripe berries of each species from each of 10 stands at random (100 berries total for each species). We froze the berries in plastic bags at –25 °C within 24 h of picking. We subsequently cleaned each 10-berry sample of all dirt, stems, sepals, and leaves; air dried the sample for 24 h; and then oven dried it for 48 h at 60 °C. We then weighed the 10-berry samples to the nearest 0.01 g on an electronic scale.

2.4. Data analysis

Five species occurred most frequently on sampled plots: bunchberry dogwood, black crowberry, false toadflax, straw-berryleaf raspberry, and lingonberry. We used berry counts of these species as response variables in separate regression analyses. However, even these species were absent from 74 to

Table 1

Berry-producing shrubs and forbs documented to occur on the eastern Kenai Peninsula, AK, USA, and included in this analysis (adapted from DeVelice et al., 1999)^a

Common name	Scientific name	Occurrence
Red fruit bearberry	<i>Arctostaphylos rubra</i>	Rare
Kinnikinnick	<i>Arctostaphylos uva-ursi</i>	Rare
Bunchberry dogwood	<i>Cornus canadensis</i>	Common
Devilsclub	<i>Oplopanax horridus</i>	Common
Black crowberry	<i>Empetrum nigrum</i>	Common
False toadflax	<i>Geocaulon lividum</i>	Common
Small cranberry	<i>Vaccinium oxycoccos</i>	Common
Stink currant	<i>Ribes bracteosum</i>	Rare
Skunk currant	<i>Ribes glandulosum</i>	Rare
Northern black currant	<i>Ribes hudsonianum</i>	Rare
Trailing black currant	<i>Ribes laxiflorum</i>	Common
Currant	<i>Ribes species</i>	–
Red currant	<i>Ribes triste</i>	Common
Prickly rose	<i>Rosa acicularis</i>	Common
Arctic blackberry	<i>Rubus arcticus</i>	Common
Cloudberry	<i>Rubus chamaemorus</i>	Rare
American red raspberry	<i>Rubus idaeus</i>	Rare
Strawberryleaf raspberry	<i>Rubus pedatus</i>	Common
Salmonberry	<i>Rubus spectabilis</i>	Common
Red elderberry	<i>Sambucus racemosa</i>	Common
Russet buffaloberry	<i>Shepherdia canadensis</i>	Rare
Greene's mountain ash	<i>Sorbus scopulina</i>	Common
Sitka mountain ash	<i>Sorbus sitchensis</i>	Common
Claspleaf twistedstalk	<i>Streptopus amplexifolius</i>	Common
Dwarf bilberry	<i>Vaccinium caespitosum</i>	Rare
Oval-leaf blueberry	<i>Vaccinium ovalifolium</i>	Common
Bog blueberry	<i>Vaccinium uliginosum</i>	Common
Lingonberry	<i>Vaccinium vitis-idaea</i>	Common
Squashberry	<i>Viburnum edule</i>	Common

^a Plant nomenclature followed U.S. Natural Resources Conservation Service (2004).

86% of plots. Each of the remaining berry species were absent from $\geq 96\%$ of plots. We therefore created an additional response variable, *other_berry_count*, by summing the berry counts of those remaining species (Table 1). Three species previously documented to occur on the eastern Kenai Peninsula (i.e., Saskatoon serviceberry [*Amelanchier alnifolia*], red fruit bearberry [*Arctostaphylos rubra*], and prickly currant [*Ribes lacustre*]) were not detected among our plots. Saskatoon serviceberries and red fruit bearberries were found to be common in other locations on the Kenai Peninsula during other years (R. DeVelice, Chugach National Forest, personal communication).

We considered the following environmental covariates as potential explanatory variables: canopy cover, overstory type, infestation level, year of infestation, land type, and land type association (Table 2). We collapsed the original 29 overstory types into 4 types: white spruce, spruce/mountain hemlock, Lutz spruce (representing all original types in which Lutz spruce had the highest cover of any of the tree species present), and mountain hemlock (representing all original types in which mountain hemlock had the highest cover of any of the tree species present, but within which there was a large spruce component).

We constructed total understory cover as three alternative explanatory variables: *other_veg*, *other_berry_cover*, and total

Table 2

Variables considered in the analysis of factors affecting berry productivity in forests infested with bark beetles on the eastern Kenai Peninsula, AK, USA

Parameter	Description
Canopy_cover	Overstory tree canopy cover as measured by digital camera
Other_berry_cover	Visually estimated understory cover of other berry species (excluding the five species treated as response variables)
Other_veg	Visually estimated understory cover of non-berry species
Other_cover	<i>Other_berry_cover</i> + <i>other_veg</i>
Overstory	White spruce White spruce/mountain hemlock Lutz spruce Mountain hemlock (reference value)
Infestation	Proportion of spruce trees infested: low (1–10%), medium (11–40%), or high (>40%); high is the reference level
Infest_year	Year of initial infestation (surveys summarized by Alaska Department of Natural Resources)
Infest_year ²	
Landassn	Mountain slopes Hills, high relief Hills, low relief (reference value) Volcanic
Land type	Frequently dissected; deeply or shallowly incised mountain slopes Forested lower side slopes Non-forested lower side slopes Alluvial fans or braided rivers Frequently dissected volcanic plateaus Marine or high relief terraces Low or high relief hills (reference value)

other_cover (designated *other_cover*). Before summing, we converted cover classes to the mid-points of the corresponding ranges of cover values. We examined each of these three variables in regression analyses, though no two were examined simultaneously in any model. Furthermore, we did not consider *other_berry_cover* as an explanatory variable when *other_berry_species* was the response variable (we expected percentage cover and count of the same group of species to be highly correlated, but the relationship was not informative).

We analyzed infestation level as low, medium, or high. We also standardized year of infestation (mean 0, variance 1) to minimize numeric problems in regression analyses, and created a related quadratic variable. To consolidate analyses we collapsed the following land type categories: frequently dissected, deeply incised mountain slopes with frequently dissected, shallowly incised mountain slopes; alluvial fans with braided rivers; marine with high relief terraces; and low relief with high relief hills.

We ordered potential explanatory variables into three groups from the most to least sensitive to management actions (i.e., management actions may influence canopy cover but would not affect land types): (1) canopy cover (*canopy_cover*), overstory type (*overstory*), and understory cover (either *other_veg*, *other_berry_cover*, or *other_cover*); (2) infestation level

(infestation), year of infestation, and its quadratic (infest_year and infest_year²); and (3) land type association (landassn) and land type (land type). We included landassn and land type to control for spatial variation in landscape position when testing for the effects of infestation and other explanatory variables with higher management weight. We treated the cover variables (canopy_cover, other_berry_cover, other_veg, and other_cover) as well as infest_year and infest_year² as continuous variables, and we treated the remaining variables as categorical variables.

We modeled berry count using log-linear regression and estimated the variance using the negative binomial distribution (Hosmer and Lemeshow, 2000). We estimated the unknown parameters by maximizing the likelihood using PROC GENMOD (SAS Institute Inc., 1998). We used an informal forward stepwise model-building approach. First, we ran univariate regressions using each explanatory variable. Individual covariates significant at $\alpha = 0.10$ were considered for inclusion in subsequent models. We considered covariates in order of their pre-assigned weight relative to management. That is, an initial model began with canopy_cover, overstory, other_berry_cover, other_veg, or other_cover; if any of these covariates were significant at the 10% level. If more than one was significant, we based the initial model on the covariate with the smallest *P*-value. We added subsequent explanatory variables, if they were individually significant, in order of their management importance. If a covariate became non-significant when added to the model, we subsequently dropped it. If addition of a less important term caused a more important term already in the model to become non-significant, we subsequently dropped the less important term. All covariates in the final model were significant at the 10% level.

We used SAS to calculate the predicted berry count for each plot and the S.E. of the linear predictor (the linear

predictor for the *i*th observation was based on a non-linear transformation). Calculation of the S.E. of the prediction relied on an approximate linearization of the data using the delta method (Hosmer and Lemeshow, 2000). Based on berry mass from samples of berries treated as response variables, we calculated means and variances and estimated production for each of the six response variables from each of the sample plots. We performed these calculations in Matlab (The Mathworks, Inc.), using SAS regression results and data from mass samples.

3. Results

Berry counts (Table 3) and mean mass of 10-berry samples varied by species or group (bunchberry dogwood = 0.08 ± 0.01 g; black crowberry = 0.20 ± 0.01 g; false toadflax = 0.65 ± 0.01 g; strawberry leaf raspberry = 0.26 ± 0.04 g; lingonberry = 0.17 ± 0.01 g; other berries = 0.67 ± 0.08 g). Based on berry counts (Table 3), we developed models for five species (bunchberry dogwood, black crowberry, false toadflax, strawberry leaf raspberry, and lingonberry) and for the combined group of other berry species. In four of five models, berry counts decreased as canopy cover increased (Table 4A–F). For example, the predicted number of bunchberries decreased by a multiplicative factor of 0.84 [$0.84 = \exp(10 \times -0.0171)$] for every 10% increase in canopy cover, assuming that all other factors remained fixed (Table 4A). Cover of other berry species appeared in four of five species models (except strawberry leaf raspberry; Table 4D). As the percentage cover of other berry species increased, the predicted number of berries of the species of interest decreased (Table 4). Similarly, the productivity of other berry species decreased as the cover of non-berry species (other_veg) increased (Table 4F).

Table 3
Number of berries (mean and S.E.) for each of five berry species and the combined counts for remaining berry species, by overstory class and spruce beetle infestation level on the eastern Kenai Peninsula, AK, USA

	Mean number of berries per plot															
	White spruce				White spruce/hemlock				Lutz spruce				Mountain hemlock			
	All ^a 170 ^b	L ^a 50 ^b	M ^a 30 ^b	H ^a 80 ^b	All 280 ^b	L 60 ^b	M 20 ^b	H 160 ^b	All 240 ^b	L 60 ^b	M 84 ^b	H 96 ^b	All 287 ^b	L 145 ^b	M 63 ^b	H 79 ^b
Bunchberry dogwood	35.3	66.4	44.8	13.1	20.3	1.8	139.5	2.5	29.9	17.7	33.7	34.2	10.6	10.1	7.8	13.7
S.E.	5.9	15.6	10.2	5.5	7.5	0.8	60.1	0.7	4.9	4.1	10.3	7.9	3.2	4.6	5.3	7.0
Black crowberry	2.3	0.9	3.2	3.1	1.5	0.0	0.0	2.7	17.2	20.6	30.6	3.3	14.0	0.3	1.8	48.7
S.E.	0.7	0.5	2.7	1.0	0.5	–	–	0.9	5.0	5.5	13.3	2.1	5.2	0.3	0.7	18.5
False toadflax	15.1	3.8	7.9	26.7	12.0	0.0	0.1	21.0	22.4	1.4	45.6	15.3	6.5	2.9	0.8	17.4
S.E.	2.8	1.6	3.7	5.6	3.7	–	0.1	6.4	5.1	0.6	12.4	6.4	1.7	1.3	0.5	5.4
Strawberry leaf raspberry	3.7	2.8	2.4	1.1	4.0	6.0	2.6	3.3	0.4	0.4	0.3	0.4	0.8	0.8	0.9	0.8
S.E.	0.9	1.4	0.9	0.5	0.8	2.3	1.5	1.0	0.1	0.2	0.2	0.2	0.2	0.2	0.4	0.2
Lingonberry	10.8	4.7	0.4	19.9	0.8	0.0	0.0	1.3	5.1	3.3	6.3	5.1	0.7	0.1	1.5	1.4
S.E.	2.8	2.2	0.2	5.6	0.3	–	–	0.6	1.4	1.7	2.6	2.4	0.3	0.0	0.9	1.0
Other berries	12.5	7.3	21.6	12.8	28.0	8.3	28.5	41.9	40.8	1.1	71.6	38.7	44.1	3.5	94.0	78.9
S.E.	3.0	3.0	11.1	4.4	7.0	7.6	28.5	11.3	9.6	0.5	21.8	14.0	14.1	1.4	33.0	43.4

^a Infestation (L: low; M: medium; H: high; All: counts across infestation levels, including plots for which infestation level was not recorded).

^b Number of plots.

Table 4
Final log-linear regression models for counts of berries, by species, on the eastern Kenai Peninsula, AK, USA

Parameter	Value	Estimate	S.E.	χ^2	P-value
(A) Bunchberry dogwood					
Canopy_cover		−0.02	0.01	7.92	<0.01
Other_berry_cover		−0.03	0.01	11.85	0.01
Overstory ^a	White spruce	0.81	0.51	33.25	<0.01
	White spruce/hemlock	−1.25	0.40		
	Lutz spruce	1.27	0.39		
Land type ^b	Mountain slopes	1.78	0.78	41.00	<0.01
	Forested slopes	−2.81	0.70		
	Non-forested slopes	2.73	0.77		
	Fans or rivers	0.69	0.74		
	Plateaus	−0.01	0.59		
	Terraces	−0.10	0.33		
(B) Black crowberry					
Canopy_cover		−0.03	0.01	18.01	<0.01
Other_berry_cover		−0.10	0.02	33.96	<0.01
Overstory ^a	White spruce	−0.52	0.62	10.43	0.02
	White spruce/hemlock	−1.65	0.65		
	Lutz spruce	0.99	0.74		
Infestation ^c	Low	−2.77	0.63	15.99	<0.01
	Medium	−1.01	0.67		
Landassn ^d	Mountain slopes	3.45	2.73	9.77	0.02
	Hills, high relief	2.81	1.15		
	Volcanic	2.77	1.92		
Land type ^b	Mountain slopes	−25.75	6987.08	28.09	<0.01
	Forested slopes	−6.25	1.50		
	Non-forested slopes	−25.11	6952.17		
	Fans or rivers	−2.50	1.36		
	Plateaus	−4.77	2.69		
	Terraces	−1.88	1.18		
(C) False toadflax					
Other_berry_cover		−0.10	0.01	54.46	<0.01
Overstory ^a	White spruce	0.08	0.52	25.43	<0.01
	White spruce/hemlock	0.11	0.57		
	Lutz spruce	2.35	0.56		
Infestation ^c	Low	−2.23	0.50	24.08	<0.01
	Medium	−1.61	0.49		
Landassn ^d	Mountain slopes	−6.93	2.09	33.99	<0.01
	Hills, high relief	−6.06	1.56		
	Volcanic	−10.04	1.84		
Land type ^b	Mountain slopes	1.45	2.29	45.95	<0.01
	Forested slopes	6.39	1.79		
	Non-forested slopes	1.78	2.09		
	Fans or rivers	8.35	1.69		
	Plateaus	6.50	1.96		
	Terraces	7.53	1.58		
(D) Strawberryleaf raspberry					
Canopy_cover		0.02	0.01	16.59	<0.01
Overstory ^a	White spruce	1.78	0.45	56.29	<0.01
	White spruce/hemlock	1.27	0.35		
	Lutz spruce	−1.47	0.38		
Landassn ^d	Mountain slopes	1.72	0.77	14.22	<0.01
	Hills, high relief	1.77	0.50		
	Volcanic	1.46	0.66		
Land type ^b	Mountain slopes	−0.06	0.92	12.47	0.05
	Forested slopes	−0.15	0.71		
	Non-forested slopes	−0.32	0.72		

Table 4 (Continued)

Parameter	Value	Estimate	S.E.	χ^2	P-value
	Fans or rivers	−0.68	0.76		
	Plateaus	−0.99	0.59		
	Terraces	−1.37	0.51		
(E) Lingonberry					
Canopy_cover		−0.02	0.01	4.40	0.04
Other_berry_cover		−0.07	0.02	17.71	<0.01
Overstory ^a	White spruce	2.37	0.54	27.21	<0.01
	White spruce/hemlock	−0.03	0.57		
	Lutz spruce	1.86	0.49		
Landassn ^d	Mountain slopes	−0.16	1.88	11.06	0.01
	Hills, high relief	0.18	0.85		
	Volcanic	−2.48	1.16		
Land type ^b	Mountain slopes	−21.71	6940.08	19.08	<0.01
	Forested slopes	−3.58	1.78		
	Non-forested slopes	−0.69	2.13		
	Fans or rivers	−1.77	1.15		
	Plateaus	−0.73	1.89		
	Terraces	0.27	0.85		
(F) Other berry species					
Canopy_cover		−0.01	0.01	6.47	0.01
Other_veg		−0.02	0.01	12.77	<0.01
Infestation ^c	Low	−1.92	0.38	28.43	<0.01
	Medium	0.81	0.45		
Land type ^b	Mountain slopes	0.33	0.86	23.12	0.01
	Forested slopes	1.26	0.79		
	Non-forested slopes	−0.61	0.87		
	Fans or rivers	−1.82	0.71		
	Plateaus	1.85	0.71		
	Terraces	−0.21	0.41		

^a Relative to the reference category for “mountain hemlock”.

^b Relative to the reference category for “low or high relief hills”.

^c Relative to the reference category for “high”.

^d Relative to the reference category for “hills, low relief”.

Overstory type was included in final models of berry counts for the five species, but not for the group of other berry species (Table 4F). We interpreted overstory relative to the reference level of mountain hemlock. For example, the coefficient for white spruce indicated that predicted number of bunchberries was 2.24 [2.24 = exp(0.8082)] times higher in plots classified as white spruce than in plots classified as mountain hemlock (assuming that all other factors remain fixed). In contrast, the predicted number of bunchberries in white spruce/mountain hemlock plots was 29% [0.29 = exp(−1.2461)] of the predicted number in mountain hemlock plots. Infestation level was a significant covariate in the final models for black crowberry (Table 4B), false toadflax (Table 4C), and for the group of other berry species (Table 4F). Berry production was typically higher where spruce dominated the overstory (Tables 5 and 6) and increased as the intensity of spruce beetle infestation increased (Table 6).

Land type appeared in all six final models. Land type association appeared in four of six final models (black crowberry, false toadflax, strawberryleaf raspberry, and lingonberry). Neither year of infestation nor its quadratic appeared in any of the final models.

Table 5

Estimated production of three berry species by overstory class on the eastern Kenai Peninsula, AK, USA

Berry species	Berry production (g/m ²)			
	White spruce	White spruce/hemlock	Lutz spruce	Hemlock
Bunchberry dogwood	2.7	0.7	4.0	0.5
S.E.	0.2	0.1	0.4	0.0
Strawberryleaf raspberry	0.9	1.0	0.1	0.3
S.E.	0.1	0.1	0.0	0.0
Lingonberry	1.9	0.1	0.9	0.1
S.E.	0.1	0.0	0.1	0.0

4. Discussion

Our findings suggest that the massive outbreak of spruce beetles on the Kenai Peninsula increased the production of berries by understory plants. Berry productivity on the eastern Kenai Peninsula generally increased with increasing levels of spruce mortality from spruce beetles, presumably due to the release of berry-producing plants from competition with

Table 6

Estimated production of two berry species by overstory class and spruce beetle infestation level on the eastern Kenai Peninsula, AK, USA

Berry species	Berry production (g/m ²)															
	White spruce				White spruce/hemlock				Lutz spruce				Mountain hemlock			
	All ^a	L ^a	M ^a	H ^a	All	L	M	H	All	L	M	H	All	L	M	H
Black crowberry	2.3	0.2	1.5	3.5	1.0	0.01	0.02	1.4	6.4	5.6	4.1	9.0	1.4	0.1	0.8	4.1
S.E.	0.3	0.0	0.4	0.4	0.2	0.0	0.0	0.3	0.6	1.0	0.7	1.2	0.2	0.0	0.2	0.7
False toadflax	13.3	3.7	4.7	22.5	30.5	80.1	0.6	18.0	44.3	0.5	26.0	87.7	4.0	0.6	2.0	12.1
S.E.	1.4	0.5	0.5	2.4	6.8	28.6	0.2	1.5	5.6	0.1	2.9	12.3	0.5	0.1	0.3	1.4

^a Infestation (L: low, M: medium, H: high, and All: counts across infestation levels, including plots for which infestation level was not recorded).

overstory spruce for light, nutrients, and water. Understory plants have been commonly reported to increase their growth following bark beetle (*Dendroctonus* spp.) outbreaks in conifer forests by utilizing newly available resources (Kovacic et al., 1985; Veblen et al., 1991; Holsten et al., 1995b; Stone, 1995). However, increased berry production in stands heavily infested by bark beetles has rarely been studied or documented (but see Stone and Wolfe, 1996). Thus, the importance of post-infestation stands to wildlife populations in terms of high relative food availability has not been recognized. Theoretical models based on the response of wildlife species to changes in habitat parameters may be used to evaluate the effects of habitat changes as a result of spruce beetle infestations and subsequent management. However, knowledge of the response of berry productivity to the effects the spruce beetle infestation often was not adequate to develop hypothetical responses (e.g., Suring et al., 1998). This lack of information had the potential to be a major impediment to comprehensive evaluations of the effects of infestations and subsequent management activities because populations of wildlife species (e.g., northern red-backed voles [*Clethrionomys rutilus*]; West, 1982) and forest uses (e.g., berry picking; von Hagen and Fight, 1999; Bowker, 2001) are interrelated with berry productivity.

We also found that berry productivity was high in stands of white and Lutz spruce, the forest types most susceptible to frequent and intense spruce beetle infestations (Werner et al., 2006). Heavily infested stands may have therefore had high relative densities of berries before the outbreak occurred. As we did not replicate measurements of berry production pre- and post-infestation by spruce beetles we cannot rule this out. However, berry productivity in this study increased as canopy cover decreased suggesting that enhanced berry productivity may have been at least a partial response to the death of overstory spruce. Increased berry production following spruce beetle outbreaks likely depended on the amount of canopy thinning resulting from the disturbance. As forest canopy of infested stands continue to open as beetle-killed spruce fall (Holsten et al., 1995b), future monitoring of berry production on our plots would directly test whether continued canopy reduction from forest disturbance by spruce beetles led to increased berry production.

Land managers on the Kenai Peninsula have responded to the recent beetle infestation with three basic management options in response to increased fire risk associated with the

increased volume of standing dead and down woody material: (1) leave infested stands unmanaged, (2) harvest dead and live trees to reduce fuels, or (3) apply prescribed burns to consume fuels under controlled conditions (Goodman and Hungate, 2006). The application of such management options in stands infested by spruce beetles may further influence the production of berries available to wildlife, subsistence users, and recreational berry pickers. Thus, we discuss our findings on individual or groups of species of berry-producing plants relative to use of berries by wildlife species and their responses to fires and timber harvest.

4.1. Bunchberry dogwood

Productivity of bunchberries increased as the canopy opened due to tree mortality resulting from the spruce beetle infestation. This effect was pronounced in white and Lutz spruce stands. Bunchberry dogwood was the most common plant species in south-central Alaska, occurring on 1059 of the 2293 locations sampled (DeVelice et al., 1999). Bunchberry dogwood has been reported to be a common species in 55–90-year-old white spruce stands that have thinned out sufficiently to allow light to reach the understory (Dyrness et al., 1986). Bunchberry dogwood peaked in abundance in the tall shrub-sapling stage (3–30 years) of white spruce forests, decreased as trees became dense (26–45 years), then increased in association with hardwoods (45–150 years), and remained constant or decreased slightly into the spruce stage (150–300 years) (Foote, 1983). Spruce grouse (*Falci pennis canadensis*) use the fruit and buds; savannah sparrows (*Passerculus sandwichensis*) and American robins (*Turdus migratorius*) eat the fruit (Martin et al., 1951; Burger, 1987). Populations of northern red-backed voles in Alaska relied heavily on the fruit production of bunchberry dogwood in all seasons, but especially in winter (Jones, 1990).

The slender and shallow rhizomes of bunchberry dogwood make it susceptible to the effects of soil disturbance associated with harvesting activities (Alaback, 1984). Bunchberry dogwood decreased in presence but increased in cover on harvested sites in Montana when compared with untreated stands (Freedman and Habeck, 1985). Bunchberry dogwood rhizomes can survive mild to moderate fires that do not remove the duff and do not heat the upper soil for an extended period so it is considered to be moderately susceptible to fire-kill (McLean, 1968; Fischer and Bradley, 1987).

4.2. Black crowberry

Black crowberry productivity was lower in white spruce and Lutz spruce stands than in stands containing mountain hemlock. Within these stands productivity increased as infestation level increased and as canopy cover decreased, similar to the findings of Matsuoka et al. (2001). Fruits of black crowberry mature from August to late fall and persist through the winter under snow cover (Viereck and Little, 1972). Black crowberry fruits are utilized as fall and winter forage by several species of birds (Martin et al., 1951; Viereck and Little, 1972; Norment and Fuller, 1997). Black bears increased their foraging of black crowberries in summer as fruits ripened with the occurrence of berries in scat increasing from 5.9% in early spring to 12.9% by late summer (MacHutchon, 1989). Black crowberry seeds were also found to be a major component of the fall diet of northern red-backed voles (West, 1982). Although these fruits provide energy to consumers, they are low in protein (<2.5%) (Pulliainen et al., 1968; Moss and Parkinson, 1975).

Black crowberry was reported to be slow to recover following fire (Viereck and Schandelmeier, 1980). Black crowberry populations did not recover 2 years after forest harvest by clearcutting and subsequent burning near Fairbanks, Alaska (Dyrness et al., 1988). Black crowberry cover was slightly less in lightly burned stands than in the control for 4 years following the Wickersham Dome Fire near Fairbanks, Alaska; in severely burned stands, it was absent for 4 years following the burn (Foote, 1983; Viereck and Dyrness, 1979). Boucher (2003) reported that black crowberry decreased after severe burns on the Kenai Peninsula. Its low growth form and small stems make black crowberry particularly vulnerable to fire (Viereck, 1982). Rhizomes of black crowberry root in the organic layer or near the mineral soil surface make them more susceptible to damage from fire (Chapin and Van Cleve, 1981).

4.3. False toadflax

False toadflax berry production was higher in white spruce and Lutz spruce stands than in stands that were dominated by mountain hemlock. Productivity increased as infestation level increased, however we did not find a strong relationship between canopy cover and productivity. False toadflax, while found in open and closed, mature white spruce and black spruce forests from 70 to over 180 years old (Dyrness and Grigal, 1979; Reynolds, 1990), may be found in its greatest abundance in open white spruce stands >250 years old (Neiland and Viereck, 1977; Viereck et al., 1993). The berries are eaten by spruce grouse and northern red-backed voles (Ellison, 1966; West, 1982).

False toadflax appeared early in post-fire succession after light to moderate fires (Foote, 1993). False toadflax forms haustoria (lateral outgrowths of the root) that connect parasitically to host roots or rhizomes (Warrington, 1970). Host genera include *Picea*, *Betula*, *Salix*, *Alnus*, and *Linnaea*. False toadflax is top-killed by most fires; survival of rhizomes is

dependent on depth of burial and fire severity (Matthews, 1994).

4.4. Lingonberry

Lingonberry production was higher in white spruce and Lutz spruce stands than in stands that were dominated by mountain hemlock. Productivity increased as canopy cover decreased. Increased lingonberry biomass was correlated with decreased canopy cover (Oldemeyer and Seemel, 1976; Ihalainen et al., 2003). Plants growing under a closed canopy rarely produced fruit or flowers, but plants growing under a more open canopy commonly produced fruit (Lehmushovi, 1977).

Lingonberries provide an important food source for birds and mammals (Hall and Shay, 1981). Berries persist over winter and provide an essential food source for birds during spring migration (Norment and Fuller, 1997). Northern red-backed voles consume large quantities of lingonberry fruit in the fall and winter (West, 1982). Lingonberry fruit is also an important food for black bears (Hatler, 1972).

Lingonberry often survives light to moderate fires, but underground propagules may be killed in severe fires (Viereck and Schandelmeier, 1980). Recovery of this species in black spruce stands 4 years after the Wickersham Dome Fire near Fairbanks, Alaska, was higher in lightly burned than in heavily burned stands (Viereck and Dyrness, 1979). Lingonberry is present 1–5 years after fire in white spruce stands, peaks in productivity from 15 to 50 years after a fire, and declines (but remains present) in later stages (Foote, 1983; Dyrness et al., 1986). Lingonberry showed a mixed response to fire on the Kenai Peninsula, decreasing on nine of 14 sites where it occurred (Boucher, 2003), possibly a response related to its rooting characteristics. It is generally shallowly rooted, but rhizomes can penetrate mineral soil (Hungerford, 1986; Smith, 1962), and it may possess a taproot (Smith, 1962).

To maintain productive populations, lingonberry may require light to moderate fire (Engelmark, 1987) or other disturbance, such as spruce beetle infestation. It commonly reestablishes on a site after fire through sprouting from rhizomes and aerial stems then increasing in cover and vigor (Bradshaw and Zackrisson, 1990). Cover and frequency of lingonberry also increased after timber harvest in mature spruce stands (Dyrness et al., 1988; Kuchko, 1988).

4.5. Strawberryleaf raspberry and other berries

Strawberryleaf raspberry productivity was greatest in white spruce and white spruce/mountain hemlock communities. Productivity increased with increased canopy cover. DeVelice et al. (1999) recorded strawberryleaf raspberry at 917 of 2293 locations sampled in south-central Alaska, the second most common plant species (after bunchberry dogwood) they encountered. Boucher (2003) reported that late-succession and forest-associated species, including strawberryleaf raspberry, decreased after burning on the Kenai Peninsula. Although this species is common, limited additional information is available on its ecological relationships.

The productivity of all other berries changed based on differences in infestation levels; mean productivity (S.E.) was 2.0 (0.1), 90.7 (11.3), and 22.6 (1.5) berries in g/m² at low, medium, and high infestation levels, respectively. Stone and Wolfe (1996) reported a similar response for frequency of fruit presence. They suggested that increased levels of irradiance increased sexual reproductive effort and reduced abortion of fruits.

5. Conclusions

Berry production was relatively high in stands recently infested by spruce beetles. However, increases in the grass bluejoint in some areas of the Kenai Peninsula (Holsten et al., 1995b) may impose significant competition to understory plants and cause declines in berry production. Following canopy reductions in spruce forests resulting from spruce beetle outbreaks, bluejoint can form dense mats that can reduce spruce seedling recruitment and growth (Liefvers et al., 1993; Holsten et al., 1995b; Goodman and Hungate, 2006). The application of specific management actions to either reduce bluejoint, speed reforestation, decrease fire risk, or recover the economic value of the dead or dying spruce may also reduce the production of berries available to wildlife and the public. Only lingonberry was expected to also increase productivity following harvest and/or prescribed burning of beetle-killed trees. Other berry species appear to respond negatively to timber harvest (i.e., bunchberry dogwood) or to prescribed burns and especially hot fires (i.e., bunchberry dogwood, black crowberry, false toadflax—the most productive species in this study). Consequently, when planning timber harvests and prescribed burns the potential effects of management activities on berry productivity need to be carefully evaluated to ensure desired outcomes.

Acknowledgments

The U.S. Forest Service, Chugach National Forest, provided funding for this project. The encouragement and support of M. Novy and S. Zemke made this study possible. T. McDonald, Western EcoSystems Technology, Inc., assisted with study design and initial data analysis. A. Poe and B. Brown assisted with data synthesis. C. Madsen developed and implemented the process for converting digital photographs to measurements of canopy cover. K. Preston assisted with aspects of study design and data processing that incorporated geographic information system analyses. This manuscript benefited greatly from the reviews of S. Matsuoka, M. Shephard, R. DeVelice and one anonymous reviewer. This study could not have been completed without the dedication and hard work of numerous biological technicians and volunteers. We thank each of you.

References

- Alaback, P.B., 1984. Plant Succession Following Logging in the Sitka Spruce–Western Hemlock Forests of Southeast Alaska. U.S. For. Ser. Gen. Tech. Rep. PNW-GTR-173. Portland, OR, USA.
- Boucher, T.V., 2003. Vegetation response to prescribed fire in the Kenai Mountains, Alaska. U.S. For. Ser. Res. Pap. PNW-RP-554. Portland, OR, USA.
- Bowker, J.M., 2001. Outdoor Recreation by Alaskans: Projections for 2000 Through 2020. U.S. For. Ser. Gen. Tech. Rep. PNW-GTR-527. Portland, OR, USA.
- Bradshaw, R.H.W., Zackrisson, O., 1990. A two thousand year history of a northern Swedish boreal forest stand. *J. Veg. Sci.* 1, 519–528.
- Burger, A.E., 1987. Fruiting and frugivory of *Cornus canadensis* in boreal forest in Newfoundland. *Oikos* 49, 3–10.
- Chapin, F.S., Van Cleve, K., 1981. Plant nutrient absorption and retention under differing fire regimes. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., Reiners, W.A. (Tech. Coords.) Fire Regimes, Ecosystem Properties: Proceedings of a Conference. U.S. For. Ser. Gen. Tech. Rep. WO-26. Washington, DC, USA, pp. 301–321.
- Cherkasov, A.F., 1974. Determining the yielding capacity of wild berries. *Rast. Resur.* 10, 253–260.
- Collins, W.B., Schwartz, C.C., 1998. Logging in Alaska's boreal forest: creation of grasslands or enhancement of moose habitat. *Alces* 34, 355–374.
- Davidson, D., DeVelice, R., 2001. Ecological subsections—Chugach National Forest. Unpubl. Admin. Paper. U.S. Forest Service, Chugach National Forest, Anchorage, AK, 13 pp.
- DeVelice, R.L., Hubbard, C.J., Boggs, K., Boudreau, S., Potkin, M., Boucher, T., Wertheim, C., 1999. Plant community types of the Chugach National Forest: southcentral Alaska. U.S. For. Ser. Alaska Reg. Tech. Pub. R10-TP-76. Anchorage, AK, USA.
- Dyrness, C.T., Grigal, D.F., 1979. Vegetation–soil relationships along a spruce forest transect in interior Alaska. *Can. J. Bot.* 57, 2644–2656.
- Dyrness, C.T., Viereck, L.A., Foote, M.J., Zasada, J.C., 1988. The Effect on Vegetation and Soil Temperature of Logging Flood-plain White Spruce. U.S. For. Ser. Res. Pap. PNW-RP-392. Portland, OR, USA.
- Dyrness, C.T., Viereck, L.A., Van Cleve, K., 1986. Fire in taiga communities of interior Alaska. In: Van Cleve, K., Chapin, III, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*. Springer-Verlag, NY, USA, pp. 74–86.
- Ellison, L., 1966. Seasonal foods and chemical analysis of winter diet of Alaskan spruce grouse. *J. Wildl. Manage.* 30, 729–735.
- Engelmark, O., 1987. Fire history correlations to forest type and topography in northern Sweden. *Ann. Bot. Fenn.* 24, 317–324.
- Ehrlich, P.R., Dobkin, D.S., Wheye, E., 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, NY, USA.
- Fischer, W.C., Bradley, A.F., 1987. Fire Ecology of Western Montana Forest Habitat Types. U.S. For. Ser. Gen. Tech. Rep. INT-GTR-223. Ogden, UT, USA.
- Foote, M.J., 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. U.S. For. Ser. Res. Pap. PNW-RP-307. Portland, OR, USA.
- Foote, M.J., 1993. Revegetation Following the 1950 Porcupine River Fire: 1950–1981. U.S. Forest Service Institute of Northern Forestry, Pacific Northwest Research Station, Fairbanks, AK, p. 71.
- Freedman, J.D., Habeck, J.R., 1985. Fire, logging, and white-tailed deer interrelationships in the Swan Valley, northwestern Montana. In: Lotan, J.E., Brown, J.K. (Compilers), *Fire's Effects on Wildlife Habitat—Symposium Proceedings*. U.S. For. Ser. Gen. Tech. Rep. INT-GTR-186. Ogden, UT, pp. 23–35.
- Goodman, L.F., Hungate, B.A., 2006. Managing forests infested by spruce beetles in south-central Alaska: effects on nitrogen availability, understory biomass, and spruce regeneration. *For. Ecol. Manage.* 227, 267–274.
- Hall, I.V., Shay, J.M., 1981. The biological flora of Canada. 3. *Vaccinium vitis-idaea* L. var. *minus* Lodd. *Supplementary Account. Can. Field-Nat.* 95, 434–464.
- Hatler, D.F., 1972. Food habits of black bears in interior Alaska. *Can. Field-Nat.* 86, 17–31.
- Holsten, E.H., Hennon, P., Wittwer, D., Matthews, K., 1995a. Forest insect and disease conditions in Alaska-1995. U.S. For. Ser. Alaska Reg. Tech. Pap. R10-TP-61. Anchorage, AK, USA.

- Holsten, E.H., Werner, R.A., DeVelice, R.L., 1995b. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environ. Entomol.* 24, 1539–1547.
- Hosmer, D.W., Lemeshow, S., 2000. second ed. *Applied Logistic Regression*, second ed., John Wiley and Sons, NY, USA.
- Hungerford, R.D., 1986. Vegetation response to stand cultural operations on small stem lodgepole pine stands in Montana. In: *Proceedings: Weed Control for Forest Productivity in the Interior West*, Cooperative Extension, Washington State University, Spokane, WA, pp. 63–71.
- Ihalainen, M., Salo, K., Pukkala, T., 2003. Empirical prediction models for *Vaccinium myrtillus* and *V. vitis-idaea* berry yields in North Karelia, Finland. *Silva Fenn.* 37, 95–108.
- Jones, E.N., 1990. Effects of forage availability on home range and population density of *Microtus pennsylvanicus*. *J. Mammal.* 71, 382–389.
- Kirchhoff, M.D., Thomson, S.R.G., 1998. Effects of selective logging on deer habitat in southeast Alaska: a retrospective study. *Alas. Dep. Fish and Game, Fed. Aid in Wildl. Rest., Res. Final. Rep., Grants W-24-4,5 and W-27-1*, Job 2.11.
- Kovacic, D.A., Dyer, M.I., Cringan, A.T., 1985. Understory biomass in ponderosa pine following mountain beetle infestation. *For. Ecol. Manage.* 13, 53–67.
- Kuchko, A.A., 1988. Bilberry and cowberry yields and the factors controlling them in the forests of Karelia, U.S.S.R. *Acta Bot. Fenn.* 136, 23–25.
- Lance, E.W., Howell, S., 2000. Survey of songbirds during a spruce beetle (*Dendroctonus rufipennis*) outbreak on the Kenai Peninsula, Alaska. *Northwest. Nat.* 81, 1–10.
- Lance, E.W., Howell, S.M., Lance, B.K., Howlin, S., Suring, L.H., Goldstein, M.I., 2006. Spruce beetles and timber harvest in Alaska: implications for northern red-backed voles. *For. Ecol. Manage.* 222, 476–479.
- Lehmushovi, A., 1977. Trials with the cowberry in Finland. *Acta Hort.* 61, 301–308.
- Lieffers, V.J., Macdonald, S.E., Hogg, E.H., 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. *Can. J. For. Res.* 23, 2070–2077.
- MacHutchon, A.G., 1989. Spring and summer food habits of black bears in the Pelly River Valley, Yukon. *Northwest. Sci.* 63, 116–118.
- Martin, A.C., Zim, H.S., Nelson, A.L., 1951. *American Wildlife and Plants. A Guide to Wildlife Food Habits*. Dover Publications, Inc., NY, USA.
- Matsuoka, S.M., Handel, C.M., Ruthrauff, D.R., 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. *Can. J. Zool.* 79, 1678–1690.
- Matthews, R.F., 1994. *Geocaulon lividum*. In: *Fire Effects Information System*, U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT <http://www.fs.fed.us/database/feis/> (online).
- McLean, A., 1968. Fire resistance of forest species as influenced by root systems. *J. Range Manage.* 22, 120–122.
- Moss, R., Parkinson, J.A., 1975. The digestion of bulbils (*Polygonum viviparum*) and berries (*Vaccinium myrtillus* and *Empetrum* sp.) by captive ptarmigan (*Lagopus mucus*). *Br. J. Nutr.* 33, 197–206.
- Neiland, B.J., Viereck, L.A., 1977. Forest types and ecosystems. In: *North American Forest Lands at Latitudes North of 60 Degrees: Proceedings of a Symposium*, University of Alaska, Fairbanks, AK, USA, pp. 109–136.
- Normant, C.J., Fuller, M.E., 1997. Breeding season frugivory by Harris' sparrows (*Zonotrichia querula*) and white-crowned sparrows (*Zonotrichia leucophrys*) in a low arctic ecosystem. *Can. J. Zool.* 75, 670–679.
- Nowacki, G.J., Spencer, P., Brock, T., Fleming, M., Jorgenson, T., 2001. *Unified Ecoregions of Alaska and Neighboring Territories*. U.S. Geological Survey Map. Open-File Report 02-297. Anchorage, AK.
- Oldemeyer, J.L., Seemel, R.K., 1976. Occurrence and nutritive quality of lowbush cranberry on the Kenai Peninsula, Alaska. *Can. J. Bot.* 54, 966–970.
- Pulliainen, E., Paloheimo, L., Syrjala, L., 1968. Digestibility of blueberry stems (*Vaccinium myrtillus*) and cowberries (*Vaccinium vitis-idaea*) in the Willow Grouse (*Lagopus lagopus*). *Ann. Acad. Sci. Fenn. Ser. A IV Biol.* 126, 1–15.
- Reynolds, K.M., 1990. Preliminary classification of forest vegetation of the Kenai Peninsula, Alaska. U.S. For. Ser. Res. Pap. PNW-RP-424. Portland, OR, USA.
- Reynolds, K.M., Holsten, E.H., 1996. Classification of spruce beetle hazard in Lutz and Sitka spruce stands on the Kenai Peninsula, Alaska. *For. Ecol. Manage.* 84, 251–262.
- Risdahl, G.L., 1984. Review of Brown/Grizzly Bear Food Habits with Inferences on the Diet of Kenai Peninsula Brown Bears. U.S. For. Ser., Chugach National Forest, Seward, AK, USA.
- SAS Institute Inc., 1998. SAS Online Document, Version 7.0. SAS Institute Inc., Cary, NC, USA.
- Schwartz, C.C., Franzmann, A.W., 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildl. Monogr.* 113.
- Smith, D.W., 1962. Ecological studies of *Vaccinium* species in Alberta. *Can. J. Plant Sci.* 42, 82–90.
- Smith, P.A., 1984. Kenai black bears and cranberries: bear food habits and densities. M.S. Thesis. University of Alaska, Fairbanks, AK, USA.
- Stone, W.E., 1995. The impact of a mountain pine beetle epidemic on wildlife habitat and communities in post-epidemic stands of a lodgepole pine forest in northern Utah. Ph.D. Dissertation. Utah State University, Logan, UT, USA.
- Stone, W.E., Wolfe, M.L., 1996. Response of understory vegetation to variable tree mortality following mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122, 1–12.
- Suring, L.H., 1998. Spruce bark beetle and wildlife. Interagency Forest Ecology Study Team—INFEST. Forest Information Series, vol. 11, <http://www.sf.adfg.state.ak.us/sarr/forestecology/fswild.cfm> (online).
- Suring, L.H., Barber, K.R., Schwartz, C.C., Bailey, T.N., Shuster, W.C., Tetreau, M.D., 1998. Analysis of cumulative effects on brown bears on the Kenai Peninsula, Southcentral Alaska. *Ursus* 10, 107–117.
- U.S. Natural Resources Conservation Service, 2004. The PLANTS Database, Version 3.5. Baton Rouge, LA, USA, <http://plants.usda.gov> (online).
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72, 213–231.
- Viereck, L.A., 1982. Effects of fire and firelines on active layer thickness and soil temperatures in interior Alaska. In: French, H.M. (Ed.), *Proceedings of the 4th Canadian Permafrost Conference, The Roger J.E. Brown Memorial Volume*, National Research Council of Canada, Ottawa, Ont., Canada, pp. 123–135.
- Viereck, L.A., Dyrness, C.T. (Eds.), 1979. *Ecological Effects of the Wickersham Dome Fire Near Fairbanks, Alaska*. U.S. For. Ser. Gen. Tech. Rep. PNW-90. Portland, OR, USA.
- Viereck, L.A., Dyrness, C.T., Foote, M.J., 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Can. J. For. Res.* 23, 889–898.
- Viereck, L.A., Little Jr., E.L., 1972. *Alaska Trees and Shrubs*. U.S. For. Ser. Agric. Handb. 410. Washington, DC, USA.
- Viereck, L.A., Schandelmeier, L.A., 1980. Effects of Fire in Alaska and Adjacent Canada—A Literature Review. U.S. Bureau Land Manage. Alaska Tech. Rep. 6. Anchorage, AK, USA.
- von Hagen, B., Fight, R.D., 1999. Opportunities for Conservation-Based Development of Nontimber Forest Products in the Pacific Northwest. U.S. For. Ser. Gen. Tech. Rep. PNW-GTR-473. Portland, OR, USA.
- Warrington, P.D., 1970. The haustorium of *Geocaulon lividum*, a root parasite of the Santalaceae. *Can. J. Bot.* 48, 1669–1675.
- Werner, R.A., Raffa, K.F., Iilman, B.L., 2006. Insect and pathogen dynamics. In: Chapin, F.S., Oswood III, M.W., van Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), *Alaska's Changing Boreal Forest*. Oxford University Press, London, UK, Published January 2006. 368 pp. ISBN 10:019515312.
- West, S.D., 1982. Dynamics of colonization and abundance in central Alaskan populations of the northern red-backed vole, *Clethrionomys rutilus*. *J. Mammal.* 63, 128–143.
- Williams, D., 1999. Response of small mammal populations to spruce bark beetle infestation and logging on the Kenai Peninsula, Alaska. M.S. Thesis. Oklahoma State University, Stillwater, OK, USA.
- Wittwer, D. (Compiler), 2004. *Forest Health Conditions in Alaska—2003*, a Forest Health Protection Report. U.S. For. Ser. Tech. Rep. R10-TP-113. Juneau, AK, USA.