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# THE INFLUENCE OF FALLEN TREE TIMING ON SPRUCE BEETLE BROOD PRODUCTION

Elizabeth G. Hebertson[1] and Michael J. Jenkins[2]

ABSTRACT.—This study compared brood production of the spruce beetle (*Dendroctonus rufipennis* Kirby [Coleoptera: Curculionidae, Scolytinae]) in downed host material felled during summer and spring seasons on the Wasatch Plateau in south central Utah. Thirty-three matched pairs of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) trees were selected for study in spring 1996. One tree of each pair was cut during August 1996 (summer-felled), and the other tree was cut in early April 1997 (spring-felled), so that trees would be colonized by spruce beetles of the same flight period. Brood adults were collected and counted from bark samples, which were removed from the top, bottom, and sides of all sample trees in October 1998. The number of emergent adults produced in June 1999 was determined from exit holes counted in bark samples removed from these same locations. Mixed-model procedures were used to compare differences in the mean number of adults produced in summer-felled versus spring-felled trees in each year. The results indicated that significantly fewer spruce beetles were produced in summer-felled trees than in spring-felled trees. More brood adults were also present in, or emerged from, unexposed bole aspects (bottom, north, and east) of sample trees than exposed aspects (top, south, and west). These findings suggest that disturbances providing spruce beetles with an abundance of fresh host material in the spring result in the greatest potential for spruce beetle production, particularly beneath unexposed bark aspects. Examples of such disturbances include snow avalanches, blowdown, and snow and ice damage.

*Key words: spruce beetle, Engelmann spruce, host material, bark beetle risk, winter disturbance, snow avalanche.*

The spruce beetle (*Dendroctonus rufipennis* Kirby [Coleoptera: Curculionidae, Scolytinae]) is a native insect of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests in the Intermountain Rocky Mountains (Furniss and Carolin 1977). Endemic populations of spruce beetles typically infest recently fallen spruce to utilize food resources in the inner bark tissues (Knight 1961, Dyer and Taylor 1971, Schmid 1977, 1981). The spruce beetle's preference for recently fallen spruce may have evolved, in part, because dead trees lack host defense responses (e.g., little resistance or hypersensitive reactions; Lieutier 2002). During winter months, snow cover also insulates the overwintering brood from lethally cold temperatures and protects them from predation by woodpeckers and squirrels (Knight 1958, 1961, McCambridge and Knight 1972, Frye et al. 1974, Schmid 1981, Werner and Holsten 1985).

Most spruce beetle outbreaks have been reported to follow extensive blowdowns or timber-harvesting operations (Miller 1970, Dyer and Taylor 1971, Schmid and Hinds 1974, Schmid and Frye 1977, Werner et al. 1977, Schmid 1981, Veblen et al. 1994). Spruce beetle populations can build in the downed host material (Lister et al. 1976) and beetles initiate attacks on healthy trees once they have depleted all resources available in the downed host material (Schmid and Frye 1977). However, the success of spruce beetle populations in downed host material depends upon the host material's suitability for colonization and brood production. Factors often associated with suitability include bark surface aspect, desiccation, temperature, and inter- and intraspecific competition (Knight 1958, Dyer and Taylor 1968, 1971, McCambridge and Knight 1972, Mitchell and Schmid 1973, Schmid 1977, 1981, Werner and Holsten 1985, Hard and Holsten 1991, Fayt et al. 2005).

Conceivably, host material created by disturbances occurring nearest to the onset of spruce beetle flight (May–June) would be less subject to deterioration caused by these factors. The greater availability of suitable habitat for spruce beetle colonization would in turn favor brood production. Conversely, exposure to sun, wind, and biotic agents could decrease

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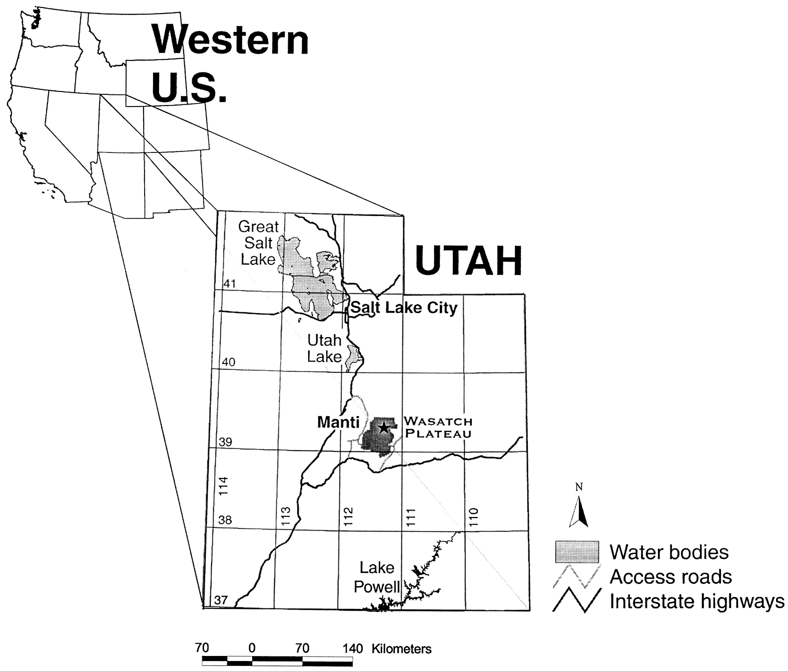


Fig. 1. Location of the study area on the Wasatch Plateau in south central Utah.

the suitability of host material created by summer and fall disturbances, ultimately limiting potential brood production.

The purpose of this study was to compare spruce beetle production in downed host material created during different seasons and thereby provide insight into the types of disturbances that may contribute to increased spruce beetle populations.

## METHODS

### Study Design

Our study area was located on the Wasatch Plateau in south central Utah (Fig. 1). This is a high mountain plateau with elevations often exceeding 3000 m. Subalpine forests comprised of mature Engelmann spruce and subalpine fir stands interspersed with subalpine meadows characterized the area. An ongoing spruce beetle outbreak was first detected on the plateau by aerial surveys in 1987.

In March 1996, we selected 33 pairs of uninfested Engelmann spruce >36 cm diameter at breast height (dbh) as sample trees. Trees of each pair were no more than 6 m apart and were similar in age, height, and dbh. A minimum distance of 10 m was kept between all sample pairs to minimize the potential for colonizing beetles to spill over into adjacent pairs during spruce beetle flight (Schmid 1981). Through the duration of the study, two 16-unit Lindgren funnel traps (Lindgren 1983) baited with $\alpha$-pinene and frontalin lures were located in the study area at least a quarter mile away from the vicinity of paired trees to monitor the beginning and completion of spruce beetle flight periods.

After spruce beetle flight ceased in early August 1996, we examined all sample trees in each pair to be sure that they had not been attacked. Spruce beetles had infested trees in 2 of the pairs, and consequently, these pairs were omitted from the study. One tree in each of the remaining 31 pairs was randomly selected and felled (hereafter referred to as summer-felled trees). The 2nd tree of each pair was felled in early April 1997 (hereafter referred to as spring-felled trees) prior to the onset of spruce beetle flight. Trees were felled in this sequence so they would be colonized by spruce beetles of same flight period. Felling constraints made it difficult to keep trees within each pair oriented in the same direction. As a consequence, pairs typically did not have the same exposure to the sun.

All trees were examined in late July 1997 to determine the developmental stage of spruce beetle larvae. The majority of larvae at this time were in their 3rd instar, indicating that they would mature in 2 years. Based on this information, we expected adult emergence to occur in spring 1999.

SAMPLING PROCEDURES, OCTOBER 1998.—Because a salvage sale was scheduled within the study area during winter 1998/1999, we first sampled all trees in October 1998. For sampling purposes, we removed a 480-cm$^2$ portion of bark from the top, bottom, and both sides of each tree at locations 1.5 m and 3 m up from the base (totaling 8 samples per tree). Over 90% of the beetles we observed within the bark samples at that time had developed into brood adults. We collected all spruce beetles and other insects from each bark sample and placed them in labeled vials. We then dissected each bark sample to remove any spruce beetles and other insects residing deeper within the bark tissues. Any pupal or larval life stages found were placed in vials containing 70% ethyl alcohol. In this sampling, we determined brood production for each tree by totaling the number of spruce beetles (including living brood adults, pupae, and larvae) counted in all bark samples collected from that tree.

SAMPLING PROCEDURES, JUNE 1999.—During winter of 1998/1999, spruce stands within the study area were logged, which resulted in the loss of 5 more tree pairs. Following spruce beetle flight in late June 1999, we used the same procedures as in October 1998 to sample the remaining 26 pairs for a 2nd time (totaling 8 samples per tree).

To determine the number of adults that emerged from each bark sample, we counted the number of exit holes. However, because individual beetles might emerge from a previously constructed exit hole (Massey and Wygant 1954, Cunningham et al. 2005), we first had to determine the number of beetles per exit hole. This was accomplished by cutting 60-cm-long bolts from trees of 5 sample pairs before spruce beetle flight in the spring of 1999 and by caging the bottom surfaces of each bolt with mesh screening to capture emerging beetles. The cages covered a bark surface area of approximately 960 cm$^2$. During emergence, beetles flew into the mesh screening and fell into a vial attached beneath the cage. We collected and counted the beetles from these vials 2–3 times per week.

At the end of the flight period, we removed the bark under each cage and counted the number of exit holes. In some cases, it was difficult to differentiate between exit holes and the variety of other holes that spruce beetles created during attack and gallery construction. Exit holes were therefore only counted if they were associated with sites of pupation. Once the number of exit holes in a bark sample had been determined, we compared it to the number of beetles collected from the corresponding cage. Using these data, we calculated the mean number of beetles to emerge per exit hole. On average, 2 and 3 brood adults emerged per exit hole from the bolts of summer-felled and spring-felled trees, respectively. We then multiplied the number of exit holes counted in bark samples collected from a given tree by either 2 or 3 to estimate the total number of adults that emerged.

### Data Analyses

We used mixed-model procedures to compare differences in the mean number of brood adults counted in October 1998 bark samples and the mean number of emergent adults estimated from June 1999 bark samples from both summer-felled and spring-felled trees. Models for each year were fit using PROC MIXED in SAS (SAS Institute, Inc. 1999). The 3 fixed-effects factors included in the model were season (2 levels: summer-felled and spring-felled), downed-tree orientation (2 levels: north–south and east–west), and aspect (3 levels: unexposed [i.e., north or east], exposed [i.e., south or west], and bottom). Because only spruce engraver beetles (*Ips pilifrons* Swaine [Coleoptera: Curculionidae, Scolytinae]) had colonized the top surfaces of trees, bark samples collected from the top surfaces were not included in the analyses. Random-effects factors included sample pairs, trees within pairs, and bark samples from trees within pairs. The data were normalized prior to the analysis using a square-root transformation. Where appropriate, Tukey-Kramer pairwise comparisons were used to test differences among main-effect means.

## RESULTS

The results of mixed-model procedures indicated that the mean number of spruce beetles that were produced in bark samples

TABLE 1. The results of mixed-model procedures for spruce beetle brood production in the 31 pairs of felled trees in October 1998.

| Source | df | Error term | *F* | *P* |
|---|---|---|---|---|
| Tests of fixed effects | | | | |
| Season | 1 | tree (pair) | 76.47 | <0.001 |
| Orientation | 1 | tree (pair) | 0.74 | 0.396 |
| Season * orientation | 1 | tree (pair) | 1.00 | 0.325 |
| Aspect | 2 | residual | 120.51 | <0.001 |
| Season * aspect | 2 | residual | 2.18 | 0.118 |
| Orientation * aspect | 2 | residual | 0.89 | 0.415 |
| Season * orientation * aspect | 2 | residual | 1.22 | 0.300 |
| Parameter | df | Estimate | | |
| Covariance parameter estimates | | | | |
| Pair | 30 | 2.38 | | |
| Tree (pair) | 28 | 0.44 | | |
| Residual | 116 | 1.81 | | |

TABLE 2. The results of mixed-model procedures for spruce beetle brood emergence in the 26 pairs of felled trees in June 1999.

| Source | df | Error term | *F* | *P* |
|---|---|---|---|---|
| Tests of fixed effects | | | | |
| Season | 1 | tree (pair) | 54.39 | <0.001 |
| Orientation | 1 | tree (pair) | 0.03 | 0.860 |
| Season * orientation | 1 | tree (pair) | 3.50 | 0.070 |
| Aspect | 2 | residual | 29.43 | <0.001 |
| Season * aspect | 2 | residual | 4.61 | 0.010 |
| Orientation * aspect | 2 | residual | 1.74 | 0.180 |
| Season * orientation * aspect | 2 | residual | 0.16 | 0.850 |
| Parameter | df | Estimate | | |
| Covariance parameter estimates | | | | |
| Pair | 26 | 0 | | |
| Tree (pair) | 24 | 1.79 | | |
| Residual | 93 | 3.86 | | |

collected in both years varied significantly ($P < 0.001$) with season and bark aspect (Tables 1, 2). The least-squares means of spruce beetle numbers in both years were significantly higher in spring-felled verses summer-felled trees (Table 3). Significantly more brood adults were also present in, or had emerged from, the bottom surfaces of sample trees compared to either unexposed (north or east) or exposed (south or west) bark aspects in both 1998 and 1999 (Tables 4, 5). Although tree orientation had no significant effect ($P > 0.05$) on spruce beetle numbers, unexposed bark aspects also produced greater mean numbers of beetles than exposed aspects in both 1998 and 1999 (Tables 4, 5). Mean spruce beetle numbers varied significantly with season and bark aspect interactions in bark samples collected in 1999 ($P = 0.01$), but not in samples collected in 1998 ($P = 0.12$; Tables 1, 2).

TABLE 3. Least-squares means for spruce beetle counts in bark samples removed from summer- and spring-felled trees in October 1998 and June 1999[a].

| Season | Mean[b] | 68% C.I. limits |
|---|---|---|
| October 1998 | | |
| Summer | 45 | 38, 42 |
| Spring | 105 | 88, 118 |
| June 1999 | | |
| Summer | 29 | 26, 32 |
| Spring | 138 | 118, 158 |

[a]Data estimated by multiplying exit hole counts of summer-felled trees by 2 and exit hole counts of spring-felled trees by 3.
[b]Adjusted $P < 0.001$.

TABLE 4. Least-squares means and differences of least-squares means by aspect for spruce beetle counts in October 1998.

| Aspect | df | Mean | 68% C.I. limits | |
|---|---|---|---|---|
| Least-squares means | | | | |
| Bottom | 116 | 38.0 | 33.7, 42.3 | |
| Unexposed | 116 | 14.0 | 11.3, 16.7 | |
| Exposed | 116 | 5.7 | 4.0, 7.4 | |
| Aspect | df | Mean | Prob. > t | Adjusted *P* |
| Differences of least-squares means | | | | |
| Bottom versus unexposed | 116 | 24.0 | <0.001 | <0.001 |
| Bottom versus exposed | 116 | 32.3 | <0.001 | <0.001 |
| Unexposed versus exposed | 116 | 8.3 | <0.001 | <0.001 |

TABLE 5. Least-squares means and differences of least-squares means by aspect for spruce beetle estimates in June 1999[a].

| Aspect | df | Mean | 68% C.I. limits | |
|---|---|---|---|---|
| Least-squares means | | | | |
| Bottom | 93 | 36.2 | 31.9, 40.5 | |
| Unexposed | 93 | 15.1 | 12.4, 17.8 | |
| Exposed | 93 | 8.8 | 6.7, 10.9 | |
| Aspect | df | Mean | Pr > t | Adjusted *P* |
| Differences of least-squares means | | | | |
| Bottom versus unexposed | 93 | 21.1 | <0.001 | <0.001 |
| Bottom versus exposed | 93 | 27.4 | <0.001 | <0.001 |
| Unexposed versus exposed | 93 | 6.2 | 0.023 | 0.060 |

[a]Data estimated by multiplying emergence hole counts of summer-cut trees by 2 and emergence hole counts of spring-cut trees by 3.

## DISCUSSION

Endemic populations of spruce beetles typically inhabit the inner bark tissues of recently fallen spruce. However, these tissues are perishable. With sufficient time, the effects of sun and wind, and the activity of animals and microorganisms can decrease the suitability of host material (Graham 1924, Knight 1958, Dyer and Taylor 1971, McCambridge and Knight 1972, Furniss and Carolin 1977, Maser and Trappe 1984, Fayt et al. 2005). The spruce beetle particularly avoids infesting dry material, and rarely attacks host material during a 2nd flight period unless it remains fresh (Dyer and Taylor 1968, Schmid 1977, 1981). With more suitable habitat available for colonization in fresh host material, spruce beetles have greater potential for brood production. Consequently, the time of year when host material is produced may influence success and growth spruce beetle populations.

In this study, we found that significantly more brood adults were present in, or had emerged from, bark samples collected from spring-felled trees compared to trees felled the previous summer. The condition of summer-felled trees at the initiation of spruce beetle flight in late May 1997 primarily explains these results. We observed that the outer bark of these trees had already begun to loosen and dry on exposed bark aspects. These symptoms were particularly prevalent on those portions of the bole that were infested by spruce engraver beetles and where foraging woodpeckers had removed the bark. Although we did not attempt to quantify interspecific competition in this study, the extent of larval galleries created by spruce engraver beetles also appeared to competitively exclude spruce beetles from a large portion of potential habitat (Nagel et al. 1957). Fungal mycelia, decay fungi, and other saprophytic organisms were also evident in the inner bark tissues of summer-felled trees by spring 1997. These organisms compete for food and also cause chemical alterations that diminish the quality of substrates for insect habitation (Graham 1924, Knight 1961, Dyer and Taylor 1971, Maser and Trappe 1984).

Conversely, the bark tissues of spring-felled trees at the beginning of flight remained generally intact and tightly adhered to the bole. Although spruce engraver beetles also infested spring-felled trees, their attacks were concurrent with spruce beetle colonization and consequently remained confined to the uppermost bole surfaces.

These findings are consistent with those of earlier studies that examined factors related to trap-tree efficacy (McComb 1953, Nagel et al. 1957). McComb (1953) indicated that trap trees felled just before or coincident with spruce beetle flight (May–June) absorbed more emergent adults than trap trees felled the previous fall. Spring felling also reduced the infestation of trap trees by spruce engraver beetles (Nagel et al. 1957).

During both years, significantly more brood adults were also present in, or emerged from, the bottoms and unexposed bark aspects of our sample trees compared to other bark aspects, irrespective of season. This result was not entirely unexpected because others have reported similar observations (Massey and Wygant 1954, Dyer and Taylor 1971, Mitchell and Schmid 1973, Frye et al. 1974, Schmid 1977, 1981). Shade and soil are assumed to buffer these aspects from high-temperature extremes and to decrease rates of evapotranspiration, both of which optimize environments for insect habitation (Graham 1924, Massey and Wygant 1954, Dyer and Taylor 1971, Schmid 1981, Maser and Trappe 1984, Werner and Holsten 1985). Thus, regardless of when disturbances create host material, the greatest spruce beetle production occurs within inner bark tissues that remain favorable for brood development and survival.

We found season and bark aspect interactions to be significant in 1999, but not in 1998. Although these findings are inconclusive, they suggest that considerably less brood production occurs beneath the unexposed aspects and bottoms of summer-felled trees because biotic and abiotic factors have had more time to reduce resource quality. Differences in host resource quality beneath various bark aspects may only be expressed in spruce beetle production beyond some critical time threshold. The availability of fresh host material in the spring may maximize suitable habitat for spruce beetles beneath all aspects.

In the Intermountain spruce-fir zone, damage caused by snow avalanches, blowdown, snow and ice breakage, and other winter disturbances can result in large quantities of downed host material for the spruce beetle (Fig. 2). Perhaps as important, winter disturbances produce host material at a time favorable for spruce beetle production. Snow cover provides moisture and protects fresh host material from the damaging effects of abiotic and biotic agents (Schmid 1977). Snowmelt generally exposes host material before or concurrent with the spruce beetle flight in the spring. Piled snow may prolong the exposure of host material in avalanche debris, allowing for colonization through the duration of spruce beetle flight. Beetles also prefer to attack shaded host material in piled logs (Schmid 1977). Snow cover and avalanche debris might also deter competing organisms from initially utilizing the resource.

The actual mechanisms responsible for triggering spruce beetle outbreaks are not well understood, and not all disturbance events result in the eruption of spruce beetle populations (Schmid 1981). Stand conditions, host vigor, climate, and existing population levels are all known to influence the initiation of outbreaks and the spread of spruce beetles through living stands (Lister et al. 1976, Schmid and Frye 1976, Werner et al. 1977, Schmid 1981, Hard 1985, Paine et al. 1997, Jenkins et al. 1998, Holsten et al. 1999, Hansen 2001, Hebertson and Jenkins 2004). However, an abundance of suitable downed host material is often necessary for spruce beetle populations to increase (Reynolds and Holsten 1994). As an important source of suitable host material for spruce beetles, winter disturbances can contribute to increased risk. Should populations reach outbreak levels in downed host material, spruce beetles may initiate attacks on living trees.

To reduce local spruce beetle risk, land managers can devise strategies to regularly monitor locations prone to winter disturbances and treat downed host material. Addressing downed spruce is particularly important in

Fig. 2. Downed woody material in the runout zone of a large avalanche in the Abajo Mountains, Utah, January 2005.

stands with moderate-to-high spruce beetle susceptibility and/or in stands with active spruce beetle populations. Preferably, land managers should remove all downed spruce from the site. Land managers can also burn or peel this material on-site, although these procedures are more costly and labor intensive. In areas with current spruce beetle activity, fresh host material may be left on site to trap dispersing adults, and then it may be removed or treated. Lands managers can also deploy funnel traps baited with spruce beetle aggregation pheromones in combination with any 1 of these treatments to contain and help absorb spruce beetle populations. Regardless of the treatment option utilized, land managers should address host material within 1 year after it is produced (Schmid and Frye 1977, Alexander 1987, Holsten et al. 1999).

## Conclusions

The results of this study indicate that the season when downed host material is created influences spruce beetle brood production. Significantly greater numbers of brood and emergent adults were produced in spring-felled trees compared to trees felled in the previous summer. More brood adults were also present in, or had emerged from, the bottom and unexposed bark aspects of all trees. However, the deterioration of host material created in the summer can reduce the availability of niches in these aspects for colonizing beetles. By creating host material at a time favorable for spruce beetle production, winter disturbances, including snow avalanches, blowdown, and snow and ice breakage, can contribute to increased spruce beetle risk.

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