Diapause and overwintering of two spruce bark beetle species

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Abstract. Diapause, a strategy to endure unfavourable conditions (e.g. cold winters) is commonly found in ectothermic organisms and is characterized by an arrest of development and reproduction, a reduction of metabolic rate, and an increased resistance to adversity. Diapause, in addition to adaptations for surviving low winter temperatures, significantly influences phenology, voltinism and ultimately population growth. We review the literature on diapause and overwintering behaviour of two bark beetle species that affect spruce-dominated forests in the northern hemisphere, and describe and compare how these strategies can influence population dynamics. The European spruce bark beetle Ips typographus (L.) (Coleoptera, Curculionidae) is the most important forest pest of Norway spruce in Europe. It enters an adult reproductive diapause that might be either facultative or obligate. Obligate diapausing beetles are considered strictly univoltine, entering this dormancy type regardless of environmental cues. Facultative diapausing individuals enter diapause induced by photoperiod, modified by temperature, thus being potentially multivoltine. The spruce beetle Dendroctonus rufipennis (Kirby) (Coleoptera: Curculionidae) infests all spruce species in its natural range in North America. A facultative prepupal diapause is averted by relatively warm temperatures, resulting in a univoltine life cycle, whereas cool temperatures induce prepupal diapause leading to a semivoltine cycle. An adult obligate diapause in D. rufipennis could limit bi- or multivoltinism. We discuss and compare the influence of diapause and overwinter survival on voltinism and population dynamics of these two species in a changing climate and provide an outlook on future research.

Key words. Dendroctonus rufipennis, diapause, Ips typographus, overwintering, Scolytines, voltinism.

Introduction

Diapause is a widespread strategy used by insects to overcome harsh conditions. An arrest of reproduction and direct development, a suppression of metabolism and an increased stress resistance are main characteristics of this dormancy type (Lees, 1956; Tauber & Tauber, 1976; Tauber et al., 1986; Danks, 1987; Denlinger, 2002; Koštál, 2006). Diapause can also affect phenology, and the response to diapause-inducing cues that can vary geographically results in variability in voltinism (i.e. the number of generations per year) among and within species (Bentz & Jónsson, 2015). The number of generations produced per year greatly influences the growth and dynamics of insect populations, which are two key factors in the management of economically important forest insect species.

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are among the most important forest pests globally. This weevil subfamily comprises approximately 6000 species of bark and wood boring insects worldwide, a group with a wide diversity...
of life histories. This includes, for example, adaptations related to reproductive behaviour, feeding modes and interactions with other organisms. Bark beetles are associated with a variety of plant taxa and their life cycles are closely tied to their hosts. Scolytines spend major parts of their life inside plants that serve as a food source, habitat for mating, development and overwintering (Wood, 1982; Kirkendall, 1983; Pfeffer, 1995; Knížek & Beaver, 2004; Bentz & Jönsson, 2015; Hulc et al., 2015). Bark beetles play important roles in forest ecosystems. They affect nutrient cycles, alter stand structure and species composition, and drive successional processes (Hansen, 2014). Moreover, their associations with other organisms, such as fungi or bacteria, contribute to biodiversity (Hofstetter et al., 2015). Several species, including those within Dendroctonus and Ips genera, can cause extensive tree mortality with significant ecological and economic impacts (Weed et al., 2013; Cognato, 2015; Raffa et al., 2015; Six & Bracewell, 2015).

Bark beetles have a particularly large influence on trees in the genus Picea, an important component of conifer forests in the northern hemisphere. The European spruce bark beetle Ips typographus (L.) (Coleoptera: Curculionidae) has a palearctic distribution (Cognato, 2015) and is the most important forest pest of Norway spruce, Picea abies, in Europe (Wermeling, 2004). The spruce beetle Dendroctonus rufipennis (Kirby) (Coleoptera: Curculionidae) infests all spruce found within its range in North America, most notably Picea glauca, Picea x luitzi, Picea sitchensis and Picea engelmannii (Holsten et al., 1999). Although in different genera, these two species of spruce bark beetle can have similar impacts on their host tree ecosystems.

The life histories of I. typographus and D. rufipennis are strongly influenced by seasonal events and they respond with similar physiological strategies. For example, both species enter diapause to buffer against harsh winter conditions and to synchronize life cycles, a widespread strategy in insects that is described for multiple bark beetle species (Ryan, 1959; Scott & Berryman, 1972; Birch, 1974; Führer & Chen, 1979; Gehrkens, 1985; Schopf, 1985; Sieber & Benz, 1985; Langor & Raske, 1987a, b; Schopf, 1989; Hansen et al., 2001a; Doležal & Sehnal, 2007; Lester & Irwin, 2012; McKee & Aukema, 2015; Gent et al., 2017). In addition, volitism of both species is influenced by differing diapause strategies.

In this review, we synthesize, summarize and compare available information on dormancy, overwintering biology and volitism of these two important insects of spruce-dominated forest ecosystems. We also discuss the influence of these life history strategies on population dynamics and the potential influence of a changing climate on future spruce bark beetle-caused tree mortality worldwide.

Ips typographus life history

Ips typographus males initially colonize a host tree and attract conspecifics using aggregation pheromones. It is a polygamous species, in which one male-usually mates with two to three females. One female beetle deposits up to 80 eggs in excavated egg niches next to the mother gallery. After larval and pupal development, tenerial beetles (i.e. freshly eclosed brood adults in the process of cuticle sclerotization prior to emergence from their natal host tree) feed on phloem tissue until matura-

Dendroctonus rufipennis life history

Although adult D. rufipennis may be observed flying from May through October, most tree attacks occur in early summer (Holsten et al., 1999), soon after temperatures become favourable for flight (Dyer, 1973; Safranyik & Linton, 1987; Holsten & Hard, 2001). It is a monogamous species with females initiating attacks on host trees and, after mating, they can deposit more than 100 eggs in two to five groups alternating on either side of the vertical mother gallery. A semivoltine life cycle (i.e. 2 years to complete a single generation) is typical throughout most of the species’ range given average weather (Schmid & Frye, 1977). Under this cycle, development proceeds through the egg and four larval instars, with the first winter passed as a diapausing prepupa (Hansen et al., 2001a). Pupation occurs approximately 1 year after host infestation followed by eclosion to teneral adults (Massey & Wygant, 1954). The second winter is passed as a teneral adult either in pupal chambers or at the base of host trees (Massey & Wygant, 1954; Knight, 1961). After the second winter, sexually mature adults emerge and disperse to attack new host trees, completing the 2-year cycle.

In years and locations with warm summers, a univoltine life cycle (i.e. one generation per year) has been observed
in Colorado (Massey & Wygant, 1954; Knight, 1961), Utah (Hansen et al., 2001b), the Pacific Northwest coast (Schmid & Beckwith, 1975), British Columbia (Dyer, 1969) and Alaska (Werner & Holsten, 1985). Under this cycle, favourable temperatures accelerate development such that the prepupal diapause is averted and pupation and eclosion to teneral adults occur before the onset of the first winter. These new brood adults then emerge and attack new hosts early the next summer, although their emergence may be delayed by up to 2 weeks compared with semivoltine beetles (E. M. Hansen, unpublished observations).

A 3-year life cycle has been observed at cold sites such as at high-elevation, northerly aspect stands that are well-shaded (Knight, 1961; McCambridge & Knight, 1972). Under this cycle, attacks on host trees may occur relatively late and/or larval development is slowed by cool conditions resulting in the first winter passed as an early-instar larva. As cool conditions prevail during the second summer, there is inadequate heat for pupation and the second winter is passed as a prepupa. Pupation and eclosion to teneral adults occur during the third summer and new brood adults emerge the next summer. A 4-year cycle has also been reported but observations were confounded by continued oviposition on hosts over consecutive years (McCambridge & Knight, 1972).

*Dendroctonus rufipennis* prefers felled hosts regardless of population phase, although eruptive populations predominantly colonize live, healthy trees (Wallin & Raffa, 2004). Large outbreaks often occur after disturbance events such as blowdown or logging operations, which allow rapid population growth in easily colonized material (Schmid & Frye, 1977), although threshold values of additional factors must also be surpassed. These include stand hazard, drought and favourable temperatures (Reynolds & Holsten, 1994; DeRose & Long, 2012; DeRose et al., 2013). Major outbreaks have occurred throughout the North American host tree range but particularly in the western part of the continent. An outbreak in Alaska during the 1990s impacted approximately 1.2 million hectares of spruce (Werner et al., 2006) and an ongoing outbreak in Colorado has affected more than 0.7 million hectares (U.S. Forest Service, 2015).

**Seasonality, dormancy and overwintering**

Phenology of both *I. typographus* and *D. rufipennis* is strongly shaped by seasonal events and fluctuations of resources. Therefore, it is crucial for an individual to time its seasonal occurrence to exploit resources efficiently and to increase the chance of survival during harsh conditions. One strategy to ensure appropriate timing with seasonal events is to undergo a developmental delay by entering a dormant state. The developmental delay achieves synchrony and sets volitism, and the dormant stage may additionally enhance survival during adversity by an increased stress resistance through physiological and behavioural preparations and by saving energy reserves through metabolic suppression (Lees, 1956; Tauber & Tauber, 1976; Tauber et al., 1986; Danks, 1987, 2006; Koštál, 2006; Hahn & Denlinger, 2007, 2011; Bentz & Jönsson, 2015).

Dormancy is a general term for a developmental and metabolic suppression and is further divided into diapause and quiescence.

Diapause is a genetically programmed, hormonally controlled response to adverse conditions and not an immediate, direct reaction to a limiting factor (i.e. quiescence) (Tauber et al., 1986; Danks, 1987; Denlinger, 2002; Koštál, 2006). Diapausing insects are not developmentally static; they develop through three main phases: (i) induction; (ii) maintenance; and (iii) termination (Koštál, 2006). Furthermore, diapause can be induced regardless of environmental signals (i.e. obligate), or flexibly induced dependent upon environmental cues (i.e. facultative) (Koštál, 2006). Facultative and obligate diapause strategies may vary both among and within species. Within species, geographical variation in diapause response allows for the efficient exploitation of resources for development and reproduction in different environments, especially in species with wide distributions (Hodek & Okuda, 1993; Winterhalter & Mousseau, 2007; McKee & Aukema, 2015; Posledovíč et al., 2015). Moreover, different dormancy strategies can also help to spread risks when uncommon and unpredictable environmental changes occur (Tauber et al., 1986; Danks, 1987).

In addition to dormancy, many bark beetle life history events are temperature-driven, including developmental rates and thresholds, survival, thresholds for the onset of swarming or feeding, and thermal sums to complete ontogenetic phases (Bakke, 1968; Bentz et al., 1991; Lobinger, 1994; Coen et al., 1996; Wermelinger & Seifert, 1998, 1999; Doležal & Sehnal, 2007; Gent et al., 2017; Schebeck & Schopf, 2017). Because winter temperatures in temperate regions frequently drop below the melting point of water, temperature also plays a major role in overwintering survival, and cold adaptations are often related to the expression of dormancy (Zachariassen, 1982; Hodek & Hodková, 1988; Denlinger, 1991; Bale, 1996; Sømme, 1999; Sinclair et al., 2003a,b; Danks, 2006; Lee, 2010).

**Diapause and overwintering of I. typographus**

Various *I. typographus* populations at different latitudes and altitudes can establish a different number of generations each year (Seitner, 1923; Kuhn, 1949; Wild, 1953; Wellenstein, 1954; Thalenhorst, 1958; Amnila, 1969; Forssé, 1991). Central European lowland populations were found to be mostly bivoltine (i.e. two generations per year) and montane, subalpine and northern European populations were observed to be mainly univoltine. However, field observations reported an absence of *I. typographus* reproductive behaviour during times of permissive environmental conditions and only the presence of immature adults late in the year (Seitner, 1923; Wild, 1953; Merker, 1957; Merker & Adlung, 1958; Amnila, 1969). For example, some populations in northern latitudes were found to be strictly univoltine, even under favourable temperature conditions for development (Amnila, 1969).

Controlled laboratory studies on the influence of photoperiod and temperature on the development of gonads and flight muscles, on physiological parameters (including respiration rates and cold hardiness) and on emergence and dispersal support an adult facultative reproductive diapause (Schopf, 1985, 1989; Doležal & Sehnal, 2007). Before *I. typographus* enters diapause, it is able to establish new generations, thus having the potential
for multivoltinism (i.e. multiple generations per year). Several laboratory and field studies suggest that a second phenotype, an obligate diapause, might also be expressed (Schopf, 1985, 1989; Netherer, 2003; Doležal & Sehnal, 2007; Dworschak, 2013; Schroeder & Dalin, 2017; N. Dobart & A. Schopf, unpublished observations). Clear evidence to distinguish between a facultative and obligate diapause could be informed through further physiological and behavioural observations (e.g. experiments at additional photoperiod and temperature conditions), but also through genomic and transcriptomic studies.

Adult facultative diapause is induced by photoperiod, modified by temperature (Schopf, 1985, 1989; Doležal & Sehnal, 2007). The critical day length varies depending on the geographical origin of a population, wherein life cycles are matched with environmental conditions. For example, beetles from Central European lowlands express a facultative diapause that is induced by a day length shorter than 15 h (Schopf, 1989; Doležal & Sehnal, 2007) and temperatures below constant 23 °C (Doležal & Sehnal, 2007). Sensitive stages for diapause induction occur late in the beetle’s life cycle (i.e. third-instar larva, pupa and adult); the development of earlier ontogenetic stages appears to be independent of photoperiod (Doležal & Sehnal, 2007). In more northern regions, diapause is induced by a longer critical day length. Along a latitudinal gradient in Sweden, beetles from a more northern origin have a critical day length of approximately 19 h, and those from a more southern population have a critical day length of approximately 16–17 h. Furthermore, diapause incidence is generally higher in more northern latitudes (Schroeder & Dalin, 2017). Termination of facultative diapause under natural conditions requires a certain chilling period that occurs in December/January in Central Europe. After diapause termination, I. typographus enters a quiescent state until conditions are permissive for gonad development and reproduction (Doležal & Sehnal, 2007).

In environments with thermal conditions that lead to a univoltine rather than a multivoltine life cycle, an obligate diapause may have evolved (Schroeder & Dalin, 2017). A proportion of beetles from some Central European populations neither emerged from breeding systems, nor dispersed, and gonads did not mature when they were exposed to permissive photoperiods and temperature conditions in the field and in the laboratory (Schopf, 1989; Netherer, 2003; Dworschak, 2013; N. Dobart & A. Schopf, unpublished observations). Adults remaining under the bark of logs at long-day conditions in the laboratory had lower metabolic rates than emerged beetles (Schopf, 1989). Thus, behavioural and physiological traits suggest that beetles expressed diapause although favourable environmental conditions prevailed. Some I. typographus from specific Scandinavian populations also enter diapause although exposed to photoperiods above the critical day length (Doležal & Sehnal, 2007; Schroeder & Dalin, 2017), including conditions >23 h light, with higher diapause ratios at a given day length in more northern regions (Schroeder & Dalin, 2017). However, the underlying mechanisms, timing of entering and terminating diapause, and influences of other environmental factors (e.g. nutritional value of the phloem tissue) are still unknown. Laboratory studies suggest that this diapause pathway could be terminated by a certain period of cool temperatures, comparable to the termination of facultative diapause (Doležal & Sehnal, 2007).

Although populations might harbour both facultative and obligate diapause phenotypes, the occurrence of each type could depend on the geographical origin of a population. An obligate diapause phenotype would predominantly be found in higher latitudes and altitudes, whereas a facultative phenotype would mainly be found in more southern regions and lower elevations (N. Dobart & A. Schopf, unpublished observations).

Furthermore, responses to diapause-inducing signals might face selective pressures and evolutionary changes might occur quickly. Diapause expression at a given photoperiod was found to differ between field caught beetles and individuals reared in the laboratory for many generations (Doležal & Sehnal, 2007; Schroeder & Dalin, 2017).

In addition to entering diapause, overwintering success at low temperatures is affected by physiological and behavioural adaptations to cope with freezing of body fluids. Ips typographus exhibits enhanced cold resistance when it develops at short day length in the laboratory (Schopf, 1985). Furthermore, metabolic suppression during diapause serves to save energy reserves during hibernation and increases the chance of survival (Schopf, 1989; Dworschak et al., 2014). However, low temperatures directly control successful overwintering of I. typographus. This species is freeze avoidant and dies when ice forms in body fluids. By accumulating cryoprotectant substances, a mixture of sugars and polyols that lower the melting point of the haemolymph, body liquids can remain fluid although the ambient temperature falls below the melting point of water (Koštál et al., 2007, 2011). This mechanism is defined as supercooling, and the temperature at which ice formation occurs is the supercooling point (SCP) (Zachariassen & Kristiansen, 2000; Lee, 2010). SCPs follow a seasonal trend where the lowest values for adults are recorded in mid-winter, approximately −25 °C in Central Europe (Schopf & Kritsch, 2010; Koštál et al., 2011) and as low as −32 °C at more northern latitudes (Annila, 1969). In general, pre-imaginal stages have higher SCPs than adults, and pupae are more resistant to cold than larvae (Annila, 1969; Schopf & Kritsch, 2010). The effects of cryoprotectants are reflected by a seasonal trend as well, similar to that of SCPs (Koštál et al., 2011). Feeding behaviour also influences resistance to cold. To increase the chance of overwinter survival, adults empty the gut before hibernation to get rid of potential ice nucleators (Annila, 1969) that can cause substantial overwinter mortality in larvae (Schopf & Kritsch, 2010).

In northern Europe, where temperatures are generally colder than in more southern latitudes, adult beetles leave the brood tree in summer and autumn to overwinter in habitats insulated by snow including in litter, soil, moss or under the bark of fallen trees (Annila, 1969). In Central Europe, I. typographus mainly overwinters under the bark of host trees (Harding & Ravn, 1985; Faccoli, 2002; Schopf & Kritsch, 2010; Wermelinger et al., 2012), although the proportion of beetles hibernating outside of trees increases with increasing elevation (Wermelinger et al., 2012). In Central European lowlands, only a small ratio of adult beetles hibernates outside the brood tree in the forest litter when ambient conditions, such as phloem quality, are unfavourable for successful overwintering (Biermann, 1977).
Regardless of the overwintering site, the ontogenetic stage for successful hibernation is the adult (Annila, 1969; Harding & Ravn, 1985; Faccoli, 2002; Schopf & Kritsch, 2010), although pre-imaginal stages can survive high sub-zero temperatures (Štefková et al., 2017). Hibernation below the snowpack, where temperatures are approximately 0°C, can increase survival, particularly in the adult stage (Annila, 1969). In the Southern Alps, although winter temperatures did not fall below −12°C, pre-imaginal stages did not survive and, regardless of the ontogenetic stage, approximately half of individuals did not hibernate successfully (Faccoli, 2002). Similar results were found in an Austrian lowland population in which all larvae and pupae died, and adult mortality was approximately 50%, although temperatures were higher than −10°C (Schopf & Kritsch, 2010).

In Southern Germany, almost all young adults survived winter and emerged in spring when they had fed before cold conditions to slightly enhance their lipid content to synthesize cryoprotectants or to maintain metabolism. Highest mortality rates were found among larvae, although winter was relatively mild with lowest temperatures of −12°C (Dworschak et al., 2014). To avoid mortality as a result of incoulative freezing (Koštál et al., 2011), adults seek relatively dry microhabitats for hibernation, such as dry litter or outer parts of the bark (Bender, 1948; Wild, 1953; Schopf & Kritsch, 2010), whereas immobile pre-imaginal stages are more likely to die from external ice formation (Schopf & Kritsch, 2010).

**Diapause and overwintering of *D. rufipennis***

Temperature has repeatedly been correlated with *D. rufipennis* developmental rates, diapause induction and subsequentvoltinism (Dyer et al., 1968; Dyer, 1970; Dyer & Hall, 1977; Werner & Holsten, 1985; Hansen et al., 2001a; Berg et al., 2006; Hansen et al., 2011). Dyer et al. (1968) estimated a lower developmental threshold of about 6°C for all life stages whereas data from Hansen et al. (2001a) suggest subtle differences in lower thresholds among life stages. Various proportions of tested individuals completed most life stages at 5.5°C, whereas the threshold for egg hatch was estimated as 7−9°C. Therefore, temperature-related quiescence should prevent development during winter and we speculate that this is the physiological mechanism for early-instar overwintering larvae among *D. rufipennis* developing on the 3-year cycle.

In contrast to quiescent larvae, prepupae and teneral adults overwinter in diapause. Several lines of evidence indicate that *D. rufipennis* prepupal overwintering results from a facultative diapause induced by relatively cool temperatures experienced during the third and fourth instars (Dyer, 1970; Dyer & Hall, 1977; Hansen et al., 2001a, 2011). For example, there is a discontinuous relationship between developmental rate and temperature in the fourth instar, suggesting that morphological and diapause development occur simultaneously during this life stage (Hansen et al., 2001a, 2011). We consider this diapause facultative because developmental delays (i.e. extended voltinism) are averted if temperatures during the first summer are sufficient for pupation.

Photoperiod has no measurable effect on prepupal diapause induction in *D. rufipennis*, which spends almost its entire life cycle in a subcortical environment (Hansen et al., 2011). In a study using *D. rufipennis* from Utah (38°37.424′N; 111°59.188′W; 3130 m elevation), larvae were reared at constant 18°C (diapause-averting) or 12°C (diapause-inducing) under short-day (LD 8:16 h) or long-day conditions (LD 16:8 h). At 18°C, total time to pupation did not significantly differ between the photoperiodic treatments (approximately 27 days) whereas none of the larvae reared at 12°C pupated regardless of photoperiod after 100 days when the experiment was ended (lower threshold for pupation ≤5.5°C). Instead, diapause has been induced in the laboratory by temperatures below 13.5−15°C during the third through late fourth instars and cool temperature exposure during the early fourth instar appears to be required for diapause-related developmental delays (Dyer & Hall, 1977; Hansen et al., 2001a, 2011). Prepupal diapause induction in *D. rufipennis* is not simply a switch that causes diapause to be expressed or not. Instead, diapause is a continuous process (Danks, 1987) and diapause-related developmental delays in *D. rufipennis* can range from just a few days to several weeks, an interval that appears sufficient to prevent pupation just before the onset of winter. The degree of delay is related to the duration of temperatures below the induction threshold, whereas the absolute temperature itself has little, if any, detectable effect (Hansen et al., 2011).

Teneral adults overwinter in reproductive diapause. Massey & Wygant (1954), studying *D. rufipennis* from Colorado, found evidence that adult overwintering may be required to attain sexual maturity. Although they did not show supporting evidence, Safranyik et al. (1990) also observed that *D. rufipennis* (presumably from Canada) overwintering as an adult is mandatory for reproduction regardless of life cycle duration and called this ‘diapause’. Attempts to rear successive generations of *D. rufipennis* from Utah at room temperature (approximately 21°C) were abandoned when the beetles did not emerge from infested bolts more than 100 days after eclosion to the adult stage (E. M. Hansen & B. J. Bentz, unpublished observations). In comparison, the entire life cycle (oviposition through adult emergence) of *Dendroctonus ponderosae* Hopkins, which has broadly similar life stage-specific developmental rates compared with *D. rufipennis* (Bentz et al., 1991; Hansen et al., 2001a), can be completed in approximately 70 days under those same conditions (Bracewell et al., 2013). However, diapause developmental delays in *D. rufipennis* may vary with geography. A proportion of adults from New Mexico (36°43.287′N; 106°15.391′W; 3034 m elevation) and Utah (40°45.660′N; 110°52.980′W; 2885 m elevation) successfully reproduce without overwintering, particularly beetles from the more southerly population (E. M. Hansen & B. J. Bentz, unpublished observations). Geographical variation in the ratio of facultative and obligate adult diapause is therefore likely and also suggests the potential for geographical variability in prepupal diapause capacity.

*Dendroctonus rufipennis* larvae and prepupae overwinter in thebole near the parent egg gallery. New adults overwinter in their pupal chambers under the bark or emerge to overwinter in the duff near the root collar of their natal host. Parent beetles frequently survive to produce sister broods in the same or the next year as determined from collections of adult beetles from logs or trees in which all broods consisted of immature stages.
and distribution patterns of several bark beetle species (Lange 2010; Bentz & Jönsson, 2015). Observations over the last some forests (Dale et al., 2001; Berg et al., 2006; Bentz et al., 2010; Bentz & Jönsson, 2015). Observations over the last decades, as well as models, found alterations of phenology and distribution patterns of several bark beetle species (Lange et al., 2006; Jönsson et al., 2007, 2009, 2011; Faccoli, 2009; Bentz et al., 2010, 2016). In addition to direct effects (i.e. the influence of temperature on development and survival) of a changing climate, indirect factors may also affect bark beetles, including alterations of host tree susceptibility and availability, competition with other species sharing the same resources, and altered interactions with organisms of various trophic levels (Bentz et al., 2010; Addison et al., 2015; Öklund et al., 2015; Schroeder & Dallin, 2017).

For _I. typographus_, recent studies found an earlier onset of swarming and thus the potential to establish more generations per year, with predictions of a shift from uni- to bivoltinism or from bi- to trivoltinism in parts of Europe (Faccoli, 2009; Jönsson et al., 2011). With higher temperatures, the lower developmental threshold could be exceeded earlier and for longer periods in a year, therefore more often surpassing the thermal sums required for the development of a full generation (Wermelinger & Seifert, 1998; Baier et al., 2007). In Europe, however, the development of more than three entire generations per year is considered unlikely (Hlášny & Turáni, 2009). Similarly, predictions for _D. rufipennis_ suggest that warming temperatures will result in a shift from semi- to univoltinism over most of its range as the prepupal diapause is averted (Bentz et al., 2010), although bivoltinism could be restricted by an obligate adult reproductive diapause. Under controlled temperatures in the laboratory, _I. typographus_ development from egg to pupation was faster than _D. rufipennis_ (Wermelinger & Seifert, 1998; Hansen et al., 2001a), confirming the increased likelihood for multivoltinism in _I. typographus_ with warming temperatures. For both species, however, as temperatures exceed optimal developmental thresholds (i.e. approximately 25 °C for _D. rufipennis_ and 30 °C for _I. typographus_), the developmental rate will slow (Wermelinger & Seifert, 1998; Hansen et al., 2011). Without evolutionary changes in developmental rates, continued warming beyond upper development thresholds will eventually result in conditions that constrain development and cause death.

Temperature also influences voltinism of both species through its effect on diapause. When the adult _I. typographus_ diapause is facultative, new generations can be initiated until inducing cues in late summer are perceived (Schopf, 1989; Doležal & Sehnal, 2007), thus contributing to the increased likelihood of multivoltinism as temperatures warm (Jönsson et al., 2011). Similarly, a facultative prepupal diapause in _D. rufipennis_ that is averted with warm summer temperatures will increase the likelihood of univoltinism (Hansen et al., 2001a, 2011). An adult obligate diapause in both species, however, could limit generation times to a strictly univoltine life cycle, despite thermal conditions favourable for development of additional generations. Assuming a mix of facultative and obligate diapausers in a population, however, the ratio of each could change as warming temperatures invoke selective pressures that favour multivoltinism and hence a facultative diapause (Danks, 1987). In addition, facultative diapausers from more southern regions could migrate northwards and lead to shifts in the composition of phenotypes (Jönsson et al., 2011). The production of sister broods can also influence the population dynamics of both species (Schmid & Frye, 1977; Anderbrant & Löfqvist, 1988; Anderbrant, 1989). In _I. typographus_,

Implications of diapause and overwintering on phenology, voltinism and outbreaks

Increased temperature and a higher chance of extreme weather events associated with climate change (IPCC, 2013) could enhance the probability of abiotic and biotic disturbances in some forests (Dale et al., 2001; Berg et al., 2006; Bentz et al., 2010; Bentz & Jönsson, 2015). Observations over the last decades, as well as models, found alterations of phenology and distribution patterns of several bark beetle species (Lange et al., 2006; Jönsson et al., 2007, 2009, 2011; Faccoli, 2009; Bentz et al., 2010, 2016). In addition to direct effects (i.e. the influence of temperature on development and survival) of a changing climate, indirect factors may also affect bark beetles, including alterations of host tree susceptibility and availability, competition with other species sharing the same resources, and altered interactions with organisms of various trophic levels (Bentz et al., 2010; Addison et al., 2015; Öklund et al., 2015; Schroeder & Dallin, 2017).

For _I. typographus_, recent studies found an earlier onset of swarming and thus the potential to establish more generations per year, with predictions of a shift from uni- to bivoltinism or from bi- to trivoltinism in parts of Europe (Faccoli, 2009; Jönsson et al., 2011). With higher temperatures, the lower developmental threshold could be exceeded earlier and for longer periods in a year, therefore more often surpassing the thermal sums required for the development of a full generation (Wermelinger & Seifert, 1998; Baier et al., 2007). In Europe, however, the development of more than three entire generations per year is considered unlikely (Hlášny & Turáni, 2009). Similarly, predictions for _D. rufipennis_ suggest that warming temperatures will result in a shift from semi- to univoltinism over most of its range as the prepupal diapause is averted (Bentz et al., 2010), although bivoltinism could be restricted by an obligate adult reproductive diapause. Under controlled temperatures in the laboratory, _I. typographus_ development from egg to pupation was faster than _D. rufipennis_ (Wermelinger & Seifert, 1998; Hansen et al., 2001a), confirming the increased likelihood for multivoltinism in _I. typographus_ with warming temperatures. For both species, however, as temperatures exceed optimal developmental thresholds (i.e. approximately 25 °C for _D. rufipennis_ and 30 °C for _I. typographus_), the developmental rate will slow (Wermelinger & Seifert, 1998; Hansen et al., 2011). Without evolutionary changes in developmental rates, continued warming beyond upper development thresholds will eventually result in conditions that constrain development and cause death.

Temperature also influences voltinism of both species through its effect on diapause. When the adult _I. typographus_ diapause is facultative, new generations can be initiated until inducing cues in late summer are perceived (Schopf, 1989; Doležal & Sehnal, 2007), thus contributing to the increased likelihood of multivoltinism as temperatures warm (Jönsson et al., 2011). Similarly, a facultative prepupal diapause in _D. rufipennis_ that is averted with warm summer temperatures will increase the likelihood of univoltinism (Hansen et al., 2001a, 2011). An adult obligate diapause in both species, however, could limit generation times to a strictly univoltine life cycle, despite thermal conditions favourable for development of additional generations. Assuming a mix of facultative and obligate diapausers in a population, however, the ratio of each could change as warming temperatures invoke selective pressures that favour multivoltinism and hence a facultative diapause (Danks, 1987). In addition, facultative diapausers from more southern regions could migrate northwards and lead to shifts in the composition of phenotypes (Jönsson et al., 2011). The production of sister broods can also influence the population dynamics of both species (Schmid & Frye, 1977; Anderbrant & Löfqvist, 1988; Anderbrant, 1989). In _I. typographus_,
the presence of sister broods in a changing climate could be more likely because parent adult re-emergence, brood establishment and development are dependent on warm conditions that may be more often met in warmer climates (Annila, 1969; Anderbrant, 1986, 1989). Sister broods are also common in D. rufipennis (Massey & Wygant, 1954) and may lead to rapid population increase (Hansen & Bentz, 2003), although more studies will be necessary to confirm this prediction. Population growth of univoltine I. typographus populations, however, will likely benefit more from sister broods than growth of multivoltine populations (Wermelinger & Seifert, 1999). In both species, assessment of sister broods and the number of generations in the field using, for example, pheromone trapping data can be difficult, as a result of a lack of distinguishing characteristics among cohorts from the same generation, as well as sister broods and generations from a previous year.

Dendroctonus rufipennis can overwinter successfully as diapausing prepupa or diapausing adult, or as a quiescent larva in the case of the 3-year life cycle (McCambridge & Knight, 1972; Hansen et al., 2001a). In contrast, only I. typographus adults can survive low sub-zero temperatures successfully (Annila, 1969; Harding & Ravn, 1985; Faccoli, 2002; Baier et al., 2007; Schopf & Kritsch, 2010; Dworschak et al., 2014). Because diapause is at least modulated by temperature, warm late summer temperatures could influence both species although in different ways. In I. typographus, warm temperatures that postpone the adult diapause induction (Doležal & Schnal, 2007; Jönsson et al., 2011) could allow a prolonged season for development and reproduction, with limited time for brood development and preparation for hibernation. Warm late summer temperatures would allow D. rufipennis to avert a prepupal diapause and therefore spend the first winter as an adult, resulting in a univoltine rather than semivoltine life cycle. Detrimental effects could also occur, however, if development proceeds to a life stage that is not resistant to severe cold, such as the pupal stage in D. rufipennis and the pre-imaginal stages in I. typographus. Prepupal (D. rufipennis) and adult (I. typographus) diapause are therefore ‘safety’ strategies to prepare for an early and abrupt onset of unfavourable conditions and to reduce the risk of mortality.

Conclusions and outlook on future research

The two bark beetle species reviewed here, I. typographus and D. rufipennis, are major disturbance agents in spruce forests globally and they employ similar strategies to survive extreme winter conditions, including diapause and resistance to cold. Differences in life stage-specific developmental rates and diapausing life stages, however, result in different phenologies with potential varying effects on voltinism and population outbreak dynamics (Table 1).

Both species can overwinter as a diapausing adult and, for I. typographus, this is the only life stage considered resistant to harsh winters. Dendroctonus rufipennis, in contrast, can also successfully overwinter as a diapausing prepupa or, less commonly, as a quiescent larva. Facultative and obligate adult diapause phenotypes that vary geographically are assumed for I. typographus and have recently also been found in D. rufipennis. Similar to the variation in adult diapause found in the closely related Dendroctonus simplex LeConte (McKee & Aukema, 2015), facultative diapause phenotypes are most prevalent in the southernmost part of each species’ distribution. Although
understanding the basis for variability among populations of these species requires additional investigation, phenotypic plasticity in diapause capacity is undoubtedly a local adaptation that mediates voltinism. For example, in *I. typographus* populations with predominately facultative rather than obligate adult diapause phenotypes, bivoltinism is possible with the potential for multivoltinism in a warming climate. Bivoltinism is currently common in southern latitude and low elevation *I. typographus* populations but has not been recorded in *D. rufipennis*. The likelihood of bivoltinism in *D. rufipennis* with climate warming is uncertain because of relatively colder habitats and slower life stage-specific developmental rates. In the coldest locations where both species may have a predominance of obligate adult diapause phenotypes, *I. typographus* populations are currently restricted to a univoltine life cycle, whereas *D. rufipennis* has a semivoltine (or longer) life cycle. A warming climate, however, may increase selection for the facultative phenotype, potentially leading to bivoltinism in *D. rufipennis* and range expansion of that life cycle in *I. typographus*.

The number of generations produced per year may have a large impact on tree mortality caused by *I. typographus* and *D. rufipennis*. Understanding the factors that influence variability in voltinism across environments, including local adaptation in diapause strategies, is therefore needed for making robust predictions across the vast ranges of both species. The influence of additional diapause terminating cues (besides temperature), including photoperiod, is still not sufficiently clear for *I. typographus* but is critical for predicting the onset of spring swarming and subsequent generation timing as winters warm. Although *D. rufipennis* adult and prepupal diapause development appears to be terminated by cold temperatures experienced in early winter, altered thermal patterns will shift the timing of adult emergence, potentially modifying the life cycle duration of the subsequent generation. Understanding similar and differing climate effects on the life history strategies of each species will inform predictions of landscape-scale impacts and global range expansion in a changing climate.

**Acknowledgements**

The present study is dedicated to the memory of Rupert Hatschek (1927–2016), who was a great patron of forest sciences in Austria. We want to thank the Austrian Science Fund (FWF) (project number: P 26749-B25) and the fund ‘Stiftung 120 Jahre Universität für Bodenkultur’ for supporting the project on diapause in *I. typographus*. There are no disputes over the ownership of the presented data. All contributions have been attributed appropriately. All authors declare that they have no conflicts of interest.

**References**

Addison, A., Powell, J.A., Bentz, B.J. & Six, D.L. (2015) Integrating models to investigate critical phenological overlaps in complex ecological interactions: the mountain pine beetle-fungus symbiosis. *Journal of Theoretical Biology*, 368, 55–66.

Amman, G.D. (1973) Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology*, 2, 541–548.

Anderbrant, O. (1986) A model for the temperature and density dependent reemergence of the bark beetle *Ips typographus*. *Entomologia Experimentalis et Applicata*, 40, 81–88.

Anderbrant, O. (1989) Reemergence and second brood in the bark beetle *Ips typographus*. *Holartic Ecology*, 12, 494–500.

Anderbrant, O. & Löfqvist, J. (1988) Relation between first and second brood production in the bark beetle *Ips typographus* (Scolytidae). *Oikos*, 53, 357–365.

Annila, E. (1969) Influence of temperature upon the development and the voltinism of *Ips* typographus L. (Coleoptera, Scolytidae). *Annales Zoologici Fennici*, 6, 161–208.

Austerlå, Ö., Annila, E., Bejer, B. & Ehnström, B. (1983) Insect pests in forests of the Nordic countries 1977–1981. *Fauna Norvegica: Series B*, 31, 8–15.

Baier, P., Pennerstorfer, J. & Schopf, A. (2007) PHENIPS – a comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology and Management*, 249, 171–186.

Bakke, A. (1968) Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. *Meddelelser fra det Norske Skogforsøksvesen*, 83, 441–602.

Bakke, A. (1983) Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. *Journal of Applied Entomology*, 96, 118–125.

Bakke, A. (1989) The recent *Ips typographus* outbreak in Norway – experiences from a control program. *Ecography*, 12, 515–519.

Bale, J.S. (1996) Insect cold hardiness: a matter of life and death. *European Journal of Entomology*, 93, 369–382.

Bender, K. (1948) Studien über die Massenvermehrung des großen Fichtenborkenkäfers (*Ips typographus* L.) aus dem Raum Messkirch (Südbaden) während der Jahre 1946 und 1947. PhD Thesis, Albert-Ludwigs-Universität Freiburg, Germany.

Bentz, B.J. & Jönsson, A.M. (2015) Modeling bark beetle responses to changing climate. *Bark Beetles: Biology and Ecology of Native and Invasive Species* (ed. by F. Vega and R. Hofstetter), pp. 533–553. Elsevier Academic Press, The Netherlands.

Bentz, B.J., Duncan, J.P. & Powell, J.A. (2016) Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate. *Forestry*, 89, 271–283.

Bentz, B.J., Logan, J.A. & Amman, G.D. (1991) Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *The Canadian Entomologist*, 123, 1083–1094.

Bentz, B.J., Régnière, J., Fettig, C.J. et al. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience*, 60, 602–613.

Berg, E.E., Henry, J.D., Fastie, C.L. et al. (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Klune National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, 227, 219–232.

Biermann, G. (1977) Zur Überwinterung des Buchdruckers, *Ips typographus* (L.), in der Bodenstreu (Col., Scolytidae). *Journal of Applied Entomology*, 84, 59–74.

Birch, M.C. (1974) Seasonal variation in pheromone-associated behavior and physiology of *Ips pini*. *Annals of the Entomological Society of America*, 67, 58–60.

Bracwell, R.R., Pfrender, M.E., Mock, K.E. & Bentz, B.J. (2013) Contrasting geographic patterns of genetic differentiation in body size and development time with reproductive isolation in *Dendroctonus*
ponderosas (Coleoptera: Curculionidae, Scolytinae). Annals of the Entomological Society of America, 106, 385–391.

Coeln, M., Niu, Y.Z. & Führer, E. (1996) Entwicklung von Fichtenborkenkäfern in Abhängigkeit von thermischen Bedingungen verschiedener montaner Waldstufen (Coleoptera: Scolytidae). Entomologia Generalis, 21, 37–54.

Cognato, A.I. (2015) Biology, systematics, and evolution of Ips, Bark Beetles: Biology and Ecology of Native and Invasive Species (ed. by F. Vega and R. Hofstetter), pp. 351–370. Elsevier Academic Press, The Netherlands.

Dale, V.H., Joyce, L.A., McNulty, S. et al. (2001) Climate change and forest disturbances. Bioscience, 51, 723–734.

Danks, H.V. (1987) Insect Dormancy: An Ecological Perspective. Biological Survey of Canada (Terrestrial Arthropods), Canada.

Danks, H.V. (2006) Insect adaptations to cold and changing environments. The Canadian Entomologist, 138, 1–23.

Denlinger, D.L. (1991) Relationship between cold hardness and diapause. Insects at Low Temperatures (ed. by R.E. Lee and D.L. Denlinger), pp. 174–198. Chapman and Hall, New York, New York.

Denlinger, D.L. (2002) Regulation of diapause. Annual Review of Entomology, 47, 93–122.

DeRose, R.J. & Long, J.N. (2012) Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. Canadian Journal of Forest Research, 42, 1649–1660.

DeRose, R.J., Bentz, B.J., Long, J.N. & Shaw, J.D. (2013) Effect of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA. Forest Ecology and Management, 308, 198–206.

Doležal, P. & Sehnal, F. (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle Ips typographus. Journal of Applied Entomology, 131, 165–173.

Dworschak, K. (2013) Ecophysiology of the European spruce bark beetle (Ips typographus L.): factors affecting individual fitness, dispersal and population dynamics. PhD Thesis, Technical University Munich, Germany.

Dworschak, K., Gruppe, A. & Schopf, R. (2014) Survivability and post-diapause fitness in a scolytid beetle as a function of overwintering developmental stage and the implications for population dynamics. Ecological Entomology, 39, 519–526.

Dyer, E.D.A. (1969) Influence of temperature inversion on development of spruce beetle, Dendroctonus obesus (Mannerheim) (Coleoptera: Scolytidae). Journal of the Entomological Society of British Columbia, 66, 41–45.

Dyer, E.D.A. (1970) Larval diapause in Dendroctonus obesus (Mannerheim) (Coleoptera: Scolytidae). Journal of the Entomological Society of British Columbia, 67, 18–21.

Dyer, E.D.A. (1973) Spruce beetle aggregated by the synthetic pheromone Frontalin. Canadian Journal of Forest Research, 3, 486–494.

Dyer, E.D.A. & Hall, P.M. (1977) Factors affecting larval diapause in Dendroctonus rufipennis (Coleoptera: Scolytidae). The Canadian Entomologist, 109, 1485–1490.

Dyer, E.D.A., Skovsgaard, J.P. & McMullen, L.H. (1968) Temperature in relation to development rates of bark beetles. Bi-monthly Research Notes—Canada, Forestry Service, 24, 15–16.

Faccoli, M. (2002) Winter mortality in sub-corticulous populations of Ips typographus (Coleoptera, Scolytidae) and its parasitoids in the south-eastern Alps. Journal of Pest Science, 75, 62–68.

Faccoli, M. (2009) Effect of weather on Ips typographus (Coleoptera Curculionidae) phenology,voltinism, and associated spruce mortality in the southeastern Alps. Environmental Entomology, 38, 307–316.

Forsse, E. (1991) Flight propensity and diapause incidence in five populations of the bark beetle Ips typographus in Scandinavia. Entomologia Experimentalis et Applicata, 61, 53–57.

Frye, R.H., Flake, H.W. & Germain, C.J. (1974) Spruce beetle winter mortality resulting from record low temperatures in Arizona. Environmental Entomology, 3, 752–754.

Führer, E. & Chen, Z.Y. (1979) Zum Einfluß von Photoperiode und Temperatur auf die Entwicklung des Kupferstechers, Pityogenes chlorographus L. (Col., Scolytidae). Forstwissenschaftliches Centralblatt, 98, 87–91.

Gehkens, U. (1985) Physiology of diapause in the adult bark beetle, Ips australis Gyll., studied in relation to cold hardness. Journal of Insect Physiology, 31, 909–916.

Gent, C.A., Wainhouse, D., Day, K.R. et al. (2017) Temperature-dependent development of the great European spruce bark beetle Dendroctonus micans (Kug.) (Coleoptera: Curculionidae: Scolytinae) and its predator Rhizophagus grandidis Gyll. (Coleoptera: Monotomidae: Rhizophaginae). Agricultural and Forest Entomology, 19, 321–331.

Hahn, D.A. & Denlinger, D.L. (2007) Meeting the energetic demands of insect diapause: nutrient storage and utilization. Journal of Insect Physiology, 53, 760–773.

Hahn, D.A. & Denlinger, D.L. (2011) Energetics of insect diapause. Annual Review of Entomology, 56, 103–121.

Hansen, E.M. (2014) Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science, 60, 476–488.

Hansen, E.M. & Bentz, B.J. (2003) Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). The Canadian Entomologist, 135, 697–712.

Hansen, E.M., Bentz, B.J. & Turner, D.L. (2001a) Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). The Canadian Entomologist, 133, 805–817.

Hansen, E.M., Bentz, B.J. & Turner, D.L. (2001b) Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). The Canadian Entomologist, 133, 827–841.

Hansen, E.M., Bentz, B.J., Powell, J.A. et al. (2011) Preupal diapause and instar IV developmental rates of the spruce beetle, Dendroctonus rufipennis (Coleoptera: Curculionidae, Scolytinae). Journal of Insect Physiology, 57, 1347–1357.

Harding, S. & Ravn, H.P. (1985) Seasonal activity of Ips typographus L. (Col., Scolytinae) in Denmark. Journal of Applied Entomology, 99, 123–131.

Hlášny, T. & Turčáni, M. (2009) Insect pests as climate change driven disturbances in forest ecosystems. Bioclimatology and Natural Hazards (ed. by K. Strelcová, C. Matyas, A. Kleidon et al.), pp. 165–170. Springer Science+Business Media BV, The Netherlands.

Hodek, I. & Okuda, T. (1993) A weak tendency to ‘obligatory’ diapause in Ips acuminatus (Coleoptera, Scolytidae) in Denmark. Entomologia Experimentalis et Applicata, 49, 153–165.

Hodek, I. & Okuda, T. (1993) A weak tendency to ‘obligatory’ diapause in Coccinella septempunctata from southern Spain. Entomophaga, 38, 139–142.

Hofstetter, R.W., Dinkins-Bookwalter, J., Davis, T.S. & Klepzig, K.D. (2015) Symbiotic associations of bark beetles. Bark Beetles: Biology and Ecology of Native and Invasive Species (ed. by F. Vega and R. Hofstetter), pp. 209–245. Elsevier Academic Press, The Netherlands.

Holsten, E.H. & Hard, J.S. (2001) Dispersal flight and attack of the spruce beetle, Dendroctonus rufipennis, in South-Central Alaska. USDA Forest Service Research Paper, 536, 1–13.

Holsten, E.H., Their, R.W., Munson, A.S. & Gibson, K.E. (1999) The Spruce Beetle. Forest Insect & Disease Leaflet 127. USDA Forest Service, Fort Collins, Colorado.

Huber, J., Atkinson, T.H., Cognato, A.I. et al. (2015) Morphology, taxonomy, and phylogenetics of bark beetles. Bark Beetles: Biology and Ecology of Native and Invasive Species (ed. by F. Vega and R. Hofstetter), pp. 41–84. Elsevier Academic Press, The Netherlands.
Safranyik, L. & Linton, D.A. (1987) Pattern of landing of spruce beetles Dendroctonus rufipennis (Coleoptera: Scolytidae) on baited lethal trap trees. *Journal of the Entomological Society of British Columbia*, **84**, 21–32.

Safranyik, L., Simmons, C.S. & Barclay, H.J. (1990) *A Conceptual Model of Spruce Beetle Population Dynamics*. Information Report No 316. Forestry Canada, Pacific Forestry Centre, Canada.

Schöbeck, M. & Schopf, A. (2017) Temperature-dependent development of the European larch bark beetle, *Ips cembrae*. *Journal of Applied Entomology*, **141**, 322–328.

Schmitt, M.-J. & Schuck, A. (2003) Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, **9**, 1620–1633.

Schmid, J.M. & Beckwith, R.C. (1975) *Model of Spruce Beetle Population Dynamics*. Information Report No 316. Forestry Canada, Pacific Forestry Centre, Canada.

Schmitz, J.M. & Frye, R.H. (1977) *Spruce Beetle in the Rockies*. General Technical Report No 49. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

Schmid, J.M. & Frye, R.H. (1977) *Spruce Beetle in the Rockies*. General Technical Report No 49. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.