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The spruce bark beetle *Ips typographus* in a changing climate

– Effects of weather conditions on the biology of *Ips typographus*

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Introductory Research Essays

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Abstract

Outbreaks of the Spruce bark beetle *Ips typographus* are often triggered by storm and drought and have destroyed millions of cubic meters of wood. It is therefore a pest insect of economic importance in Europe. Breeding underneath the bark of Norway spruce *Picea abies, I. typographus* brings blue-stain fungi into the wood which strangles the water uptake and lowers the timber quality. *I. typographus* (Coleoptera; Scolytinae) and other insects are dependent on the temperature for their metabolism and development. In a future warmer climate we may see increased storm frequencies with larger windthrows serving more breeding material for bark beetles. Further, a higher mean temperature allowing earlier onset of flight of spruce bark beetle in spring, and a faster development from egg to adult, will increase the probability of a second swarming period during the summer and production of a 2nd generation. In a warmer climate higher evaporation will lead to water shortage and increased host susceptibility, especially later during the summer. Thus, an extended (2nd) flight period may lead to more damage to spruce forests. Two generations of the spruce bark beetle is the rule in lower altitude areas of central Europe and in a future climate bivoltinistic behavior is predicted to become more common also in higher altitudes and northward in Scandinavia.

Introduction

Insects are ectothermic organisms, known as cold-blooded, which means that their body temperature is controlled by external means. As a result insects are dependent on air temperature for the metabolism and development (Huey and Kingsolver 1989). The characteristics that make insects so evolutionary successful are their ability to fly, an external skeleton, metamorphosis and a specialized system of reproduction (Mitton and Sturgeon 1982). There is more than one million insect species named, which is estimated 10-30% of the actual species number, beetles *Coleoptera* are the largest order of insects comprising of 350 000 species (Resh and Cardé 2003).

Tree-killing bark beetles

Around 6000 species of bark beetles (Coleoptera; Scolytinae) are described, but only a few species are sometimes able to kill healthy trees (Raffa et al. 2008). Among these are *Dendroctonus* species in North America and especially Mountain pine beetle *Dendroctonus ponderosae* is a big threat to the forestry (Amman 1977). In Europe, the spruce bark beetle *Ips typographus* is the most economically important forest pest (Christiansen and Bakke 1988). Nevertheless, in absence of human exploitation bark beetles participate in the decomposition of dead wood material and thus be a part of the nutrient cycling and long term productive capacity of the ecosystem and a regeneration of climax forest (Christiansen et al. 1987).

Tree killing bark beetles are characterized by their use of chemical communication, involving aggregation pheromones, and by their association with blue stain fungi which participate in exhausting the defense of the host tree (Raffa and Berryman 1983; Christiansen et al. 1987). Both aggregation and anti- aggregation pheromones have been identified. In *I. typographus* and other *Ips* species, but unlike *Dendroctonus* bark beetles, males are the major producers of pheromones (Christiansen and Bakke 1988). After releasing attracting aggregation pheromones when females entered the gallery anti-aggregation pheromones are released and they seem to regulate attack density and shift the attack to neighboring bark surface or tree (Christiansen and Bakke 1988).

Secondly all these species are associated with virulent fungi (Paine et al. 1997). The fungi are inoculated by the beetle to the phloem and may help in strangling the water transport in the xylem (Paine et al. 1997). The importance of the fungi for the actual "tree-killing" are however under debate (Six and Wingfield 2011).

The third characteristic for the aggressive bark beetle species is a high resistance to high resin flow and other chemical tree defense reactions (Christiansen and Bakke 1988).

Biology of *Ips typographus*

The spruce bark beetle (*Ips typographus)* is one of the most destructive pests to spruce forest in Europe and Asia (Christiansen and Bakke 1988). *I. typographus* starts flying in spring during the first warm days when temperature exceeds 20°C. The beetles disperse in the forest in search for suitable breeding material. Under endemic (non-outbreak) conditions they breed underneath the bark of newly dead or dying Norway spruce trees *Picea abies* and unbarked timber. The male initiates gallery construction by excavating a nuptial chamber in the phloem and after that the male emits aggregation pheromones attracting conspecifics of both sexes to the site (Christiansen and Bakke 1988). The male attracts 1- 4 females to create a polygamous gallery system. After mating each female can, at low attack densities (Anderbrant 1990), lay up to 80 eggs (Wermelinger 2004) in niches along their gallery, after more than three weeks time the parental beetles leave their 1st brood to initiate a sister brood. When the 1st brood is fully developed it will either fly and initiate a 2nd generation, or fly and maturation feed and go to hibernation, or go to hibernation in the soil, or stay under bark, all depending on not only the thermal conditions but also the photoperiod. In central Europe the rule is a fully developed 2nd generation and several sister broods while in northern Europe and Sweden the common case is one generation and one (or several) sister broods. This will be discussed more in detail under heading "Voltinism". An Outbreak (epidemics) of *I. typographus* shows a drastic change in behavior when the beetle is able to colonize and kill growing trees. Outbreaks are frequently either initiated by storm felling (abundance of defenseless breeding substrate) or triggered by drought (weakened host) or a combination of both.

Outbreak history of *Ips typographus* in Sweden and central Europe

Throughout the history, outbreaks of *I. typographus* have lead to destruction of millions of Norway spruce trees, reducing the quality of the wood as resource for timber or pulp production to a large economic value in Sweden. In 1960-2010 three major outbreaks of *I. typographus* have occurred in Sweden resulting in 9 million m^3 of killed Norway spruce (Kärvemo and Schroeder 2010). All these outbreaks were initiated by storm fellings providing large amounts of wind-thrown trees as breeding material. In the entire Europe, only during the 1990s more than 32 million m^3 of spruce forest was killed (Grégoire and Evans 2004).

Outbreaks of *I. typographus* documented in Sweden during 1930-2010:
1930s: Three storms in 1931 and 1932 resulted in 5.5 million of wind-throws in south- and central Sweden (Trägårdh and Butovitsch 1935) and *I. typographus* outbreaks was recorded in Nås, Dalarna, 1935-1938 (Butovitsch 1938) and in northern Uppland, 1932-1935 (Butovitsch 1941).

Nov 1945: A storm blew down 1 million m^3 of forest mostly in central Sweden (Värmland, Dalarna, Hälsingland and Gästrikland) (Holmberg 2005). The effects of the storm was studied in a 315 ha area of Gruvskogen, Gästrikland where 9362 spruces were blown down. In the years following the storm no management was done to reduce bark beetle damage and during 1947-1952 all together 20.111 spruces were killed by *I. typographus* (Lekander 1972). So this is an example of the natural process of an *I. typographus* outbreak.

Jan 1954: 12 million m^3 was storm-felled in central Sweden from Uppland southwards to Jönköping (Lekander 1955). Most of the timber was treated with DDT in the summer and there was no propagation of bark beetles during the next year (Lekander 1956). Apart from in Gästrikland and southeastern Dalarna which in summer 1956 experienced outbreaks of a size that motivated forest protection actions (Lekander 1957, unpublished report). In summer 1957 a trap tree campaign was performed using Lekanders method (Lekander 1952) where 4514 standing trap trees (one per in recent year beetle killed tree) were girdled and treated with a systemic insecticide. During the summer 1957 the trap trees was inspected and the treatment was found to be successful, i.e. the bark beetles were killed (Lekander 1957, unpublished report).

1970s: Central Sweden and also southern Norway was hit by a storm in 1969 that damaged 2 million m^3 of spruce forest in Norway (Ehnström et al. 1974) and 37 million m^3 in Sweden (Holmberg 2005) resulting in 5 million m^3 killed by *I. typographus* in Norway (Bakke 1989) and another 4.5 million m^3 in Sweden (Eidmann 1983; Risberg 1985) during a 12-year period which included two warm and dry summers. Worth noting is that in a large area of Sweden affected by the storm there was no epidemic of *I. typographus.* Most of the bark beetle damage was concentrated to Dalarna and Värmland (Ehnström et al. 1974). Here, beetle populations were elevated due to, apart from drought, probably human activity such as neglected forest hygiene i.e. widespread storage of pulpwood along forest roads in spring and summer (Eidmann 1983). In Norway there were three regionally separated outbreaks of different character. One area with the severe windfall in 1969 as the main causal factor, the other area with lowered host tree resistance due to drought and in the third area both windfall and drought contributed to initiate the beetle attacks (Worrell 1983).

1990s: After a warm and dry summer 1992 an increased activity of *I. typographus* started all over Sweden (Samuelsson and Örlander 2001). Kärvemo and Schroeder (2010) estimated the total volume of killed trees during the decade in southern Sweden to about 1.5 million m^3 based on reports from the Swedish forest agency.

2005-2010: Southern Sweden was hit by storms in 2005 (Gudrun) (Anon. 2006) and in 2007 (Per) (Långström et al. 2009). Since both storms occurred in January most of the trees were managed to be removed from the forest before swarming in spring. Gudrun was the largest storm-felling in Sweden in modern history causing destruction of 75 millions of m^3 of wood. Per blew down another 12 million m^3. Following the storms (2005-2010), 3.5 m^3 of spruce forests in southern Sweden have been killed by *I. typographus*. (All the above figures are based on the surveys and estimates by the Swedish Forest Agency; Skogsstyrelsen).

Some examples of outbreaks of *I. typographus* documented in central Europe during 1930-2010:

Late 1940s: After World War II in an outbreak killed some 30 million m^3 of Norway spruce in Germany and lasted for up to seven years (Schwerdtfeger 1957). To this point, this was the largest outbreak of reliable data records (Christiansen and Bakke 1988). In northern Germany this was due to bad forest sanitation because of lack of label and destroyed infrastructure after the war. In southern Germany the cause was wind and snow damage followed by several warm and dry summers in 1942-1949 (Christiansen and Bakke 1988).

2000s: Triggered by the storm in Dec 1999 (Lothar) and further enhanced by summer drought in 2003 (Forster and Meier 2009) an ongoing outbreak of *I. typographus* in central Europe 2000-2010 killed only in Austria and Switzerland together more than 30 million m^3 of spruce forest (Krehan et al. 2010; Steyrer and Krehan 2011). It seems to be an obvious coherency between damage by storm or snow and the extent of bark beetle damage (Krehan et al. 2010).

Weather effects on the biology of *Ips typographus*

Weather effects such as temperature, rainfall and sunshine strongly affect the flight activity and development of *I. typographus* and have lately been subject to a number of studies (Wermelinger and Seifert 1998; Baier et al. 2007; Faccoli 2009).

Start and duration of main flight period

The adults of the parental generation leave their overwintering sites in spring. In its northern range it is more common that *I. typographus* overwinters in the soil while in central and southern Europe it is more common to overwinter under bark in standing trees (Christiansen and Bakke 1988). In a storm-felled area in southern Sweden ~50 % of the population overwintered in the soil (Komonen et al. 2011).

The first flight takes place when certain thermal requirements needed for the maturation process are fulfilled and the air temperature reaches above 16.5°C (Lobinger 1994). Anyhow, weather conditions greatly affect the time of flight commencement. A study in Finland showed that beetles hibernating in the soil needed several days with temperatures exceeding 20°C to emerge and fly (Annila 1969). The maturation process is temperature dependent, as beetles kept at -5°C until end of April and then exposed to 10°C needed two weeks to become flight mature and when kept at 25°C beetles started to fly only after a couple of days (Forsse and Solbreck 1985).

The beetles fly in spring searching for suitable host trees. The optimum flight temperature is 22 -26°C (Wermelinger 2004). Apart from air temperature the swarming depends greatly on the amount of sunshine. Even a short sunburst will increase the number of flying beetles (Wermelinger 2004). Roughly 10% of the population seems to fly above the canopy and can take advantage of the wind to move up to 55 km in 3 hours time (Forsse and Solbreck 1985). There is also large variation in flight duration between individuals, 25% of the beetles fly for more than one hour. In a study by Forsse and Solbreck (1985) the longest recorded flight without pausing was for more than 6 hours.

The main flight of *I. typographus* in Europe generally occurs between April – June depending on latitude and altitude (Christiansen and Bakke 1988). According to Annila (1969) main flight starts from 48 dd (day-degrees) >5°C, for beetles hibernating under bark, to 170 dd >5°C, for beetles hibernating in soil (Table 1). In central Sweden the swarming normally begins from the end of May to early June (Butovitsch 1938). Trägårdh (1939) recorded flight from mid May in Gammelkroppa, Sweden in 1918. Butovitsch (1938) gives a record on early swarming in Nås, central Sweden on 4 May, 1937. Annila (1969) calculated the temperature sum to 51 dd >5°C in Nås at the above date. In the outbreak in 1970s *I. typographus* was trapped in southeastern Norway in early May in 4 out of 5 years in 1971-1975. While in 1973 the first flight began in the middle of May (Bakke et al. 1977). Corresponding data for Sweden is lacking, but in 1972 flight in southern Sweden was observed in early May, which was considered exceptional (Bo Långström pers. comm.). In central Europe the swarming begins earlier than in Fennoscandia. Untimely emergence of *I. typographus* prior to mid April is suppressed by short–day photoperiods (Dobart 2006). In Hochschwarzwald (785-1200 m.a.s.l.), southern Germany, the swarming in 1947-1951 differed between 14 April to 25 May (Wild 1953). In Denmark swarming normally starts in the middle of May; 17 May in 1980 at 103 dd >5°C and 9 May in 1981 at 68 dd (Table 1) (Harding and Ravn 1983). However, there is a large local variation for the date of emergence and flight. In a northeast-facing slope in Norway there is even records on emergence from soil as late as the middle of July (Austarå et al. 1993). In recent years, there is evidence of a shift towards earlier swarming, 20 days sooner from 1996-2005 in the southeastern Alps of Italy (Faccoli 2009).

Sister brood flights

After the parental beetles have mated and females finished laying eggs they may reemerge from underneath the bark to initiate a 2nd brood – a so called sister brood. The residence time of parental beetles is both temperature- (Annila 1969; Anderbrant 1986; Anderbrant 1989) and density-dependent (Anderbrant et al. 1985; Anderbrant 1986). The parental beetles stay shorter time under the bark at favorable conditions (warmer) and when experiencing more intraspecific competition at higher attack densities. Thus, the thermal sums estimating the reemergence is accumulated since the brood was established. In Sweden Anderbrant (1986) found that the temperature sum threshold was 168 dd > 7.5°C for the mean reemergence when breeding density was 300-400 ♀/m^2 in exposed trees (table 1). Annila (1969) gives 150-200 dd >5°C for the reemergence. The Austrian PHENIPS model gives a higher temperature sum, 278 dd > 8.3°C for reemergence of parental beetles (Wermelinger and Seifert 1998; Baier et al. 2007).

The parent beetles reemerge mainly on days with temperature exceeding 20°C (Annila 1969) and for successful colonization of living trees the beetles seem to require a period of several warm days during the main reemerging period. The males emerge before the females (Annila 1969). In south Norway 60-85% of the parent beetles had left the tree within 2-3 weeks of initial attack (Bakke 1983). Anderbrant (1989) estimates that only one third of the beetles produce a second sister brood, based on calculations on the number of attacked trees and estimated reemergence in a forest in south Norway. In the southern Alps of Italy the long summers allows most of the beetles to reemerge several times (Faccoli and Stergulc 2004). However Wermelinger and Seifert (1999) hypothesize according to linear modeling of the potential population growth that sister broods in lower elevations with up to three generations of *I. typographus* and low winter mortality only have moderate impact on the overall population growth. Further, they propose that the sister brood flight is most important for the propagation of *I. typographus* in Scandinavia and areas at higher elevations of central Europe where only one generation per year is possible. This corresponds well with the outbreak pattern of *I. typographus* in Nås, Sweden, in the late 1930s. A constant level of flight activity, infestation of new trees during the summer and observations of all developmental stages from egg to imago under bark in September in 1936 was hypothesized to be due to a sister brood flight (Butovitsch 1938). During the outbreak in Norway in 1970s estimates on infested logs some weeks after initial attack showed that more than 90% of the parent beetles is leaving their galleries (Bakke et al. 1977). This happened earlier when densities were higher which supports that sister broods are more frequent at high densities which are common during outbreaks. Thus, Anderbrant seems to have underestimated the propensity for sister broods (compare one third with 90%).

Development

The developmental time is highly depending on the temperature conditions under the bark within the brood tree which varies both with the external temperature and with the degree of exposure to sun. Higher temperatures are generally favorable and shorten the developmental time from egg to imago. But the phloem may reach temperatures higher than 47°C, which in field- (Wild 1953) and in laboratory studies (Annila 1969) been proved to be lethal. In Switzerland, Wermelinger and Seifert (1998) used the "sandwich method" (a bark sample between two Plexiglas panes) in laboratory under constant temperatures to compute the lower developmental thresholds to respectively: 10.6°C for egg, 8.2°C for larvae, 9.9°C for pupae and 8.3°C for the whole preimaginal development from egg to pupae. However, in Finland, Annila (1969) observed that all stages had undergone some development at 5°C and therefore used this temperature as a threshold for calculating the thermal sums of *I. typographus*. For the whole development from egg to adult the PHENIPS model (Baier et al. 2007) uses a threshold from Wermelinger and Seifert (1998) of 334 dd >8.3°C for the preimaginal development and 557 dd >8.3°C including the maturation feeding of filial beetles (Table 1). Further, PHENIPS uses regional topography and local air and bark temperature to predict bark beetle development at stand/tree level (Baier et al. 2007). In Finland, Annila (1969) studied the influence of sun exposure on the development using 5 trees with different aspects (sun exposed, northern edge of clearing, within stand, etc.) and the first callow adult under bark was in average observed after 342 dd >5°C (442 dd >5°C when measuring accumulated heat under bark instead of in the air) . In Denmark, the average (1980-1981) emergence of the 1st brood was slightly earlier in exposed positions (573 dd >5°C) than in the shaded positions (685 dd >5°C) (Harding and Ravn 1985).

Table 1. Thermal sums (day-degrees accumulated in the air) at different population development stages for the spruce bark beetle *Ips typographus* (parentheses show approximate values for recalculations to 5°C threshold). The development range is expanding from exposed to shaded positions.

Reference	Annila (1969)	Harding and Ravn (1985)	Anderbrant (1986)	Wermelinger & Seifert (1998); Baier et al. (2007)
Data source	field	field	lab validated in field	lab validated in field
Period	1964-1967	1980-1981		2001-2003
Temp treshold (°C)	>5	>5	>7.5 (>5)	>8.3 (>5)
1st flight	48-170			61 ±19 (100)
Sister brood flight	150-200		158-262 (240-390)	278 (460)
1st generation:				
-callow beetles under bark	342 (442*)			334 (550)
-mature beetles emerge		526-692		557 (920)
Voltinism	univoltine	uni/bivoltine		bivoltine

*thermal sum measured under bark

Voltinism

As for many other insect species, *I. typographus* voltinism depends both on thermal and photoperiodic thresholds and varies over the geographical range according to the days needed to complete development to the stage suitable for surviving hibernation (imago). However, in agreement with observations on multiple voltinistic strategies in some outbreak prone populations of *I. typographus* (Netherer and Pennerstorfer 2001) the degree-sum at which a voltinistic change is adaptive will vary with other ecological factors such as density dependence (affecting the emergence of the new generation), seasonal variation in mortality and resource availability (Kausrud 2010). In northern Europe *I. typographus* is mainly univoltine (Lange et al. 2006; Jönsson et al. 2007) while in central Europe *I. typographus* is mainly bivoltine (Wermelinger 2004). In the southern Alps there has been reports of a 3rd generation although Faccoli (2009) argues that it is limited by the summer photo period (see next paragraph) rather than by temperature. The known observations of bivoltinism in Fennoscandia are sparse. In Sweden in the 1930s initiation of a 2nd generation was recorded (Trägårdh and Butovitsch 1935; Butovitsch 1938) but no further developmental studies were undertaken. A completed 2nd generation has only been recorded in 1975 in southern Norway (Austarå et al. 1977), 2006 in southern Sweden (Långström et al. 2009) and 2010 in Finland (Pouttu and Annila 2010). In southern Norway in 1975, the thermal sum was only sufficient for a successful development of 2nd generation in lying but not standing trees (Austarå et al. 1977). Though, in Sweden 2006 a favorable thermal sum for development of a 2nd generation (Annila 1969; Harding and Ravn 1985; Wermelinger and Seifert 1998; Baier et al. 2007) of 1100 day degrees >8°C was exceeded (Långström et al. 2009). In southern Finland swarming started on 12 May in 2010, followed by a unusually warm and dry July favoring a second flight period, consequently callow beetles could be seen under the bark in October (Pouttu and Annila 2010). In Denmark Harding and Ravn (1985) discovered that even in a year with subnormal temperatures the flight activity of the new generation of *I. typographus* was intense in July and August and partly a 2nd generation was developed. Consequently in Denmark *I. typographus* is to be considered as bivoltine.

Diapause and hibernation

Hibernation in *I. typographus* is controlled by day length and temperature, initiated by long and cold nights inducing diapause (Doležal and Sehnal 2007). In central European populations diapause is induced by day length decreasing below 16 h. In the diapausing adults neither gonads nor the flight muscles matured and no swarming occurred (Doležal and Sehnal 2007). *I. typographus* hibernates in the adult stage, either in the bark of a standing or lying tree or in the forest litter close to the tree where it developed (Christiansen and Bakke 1988). In northern Europe *I. typographus* overwinters underneath the snow cover in the soil (Annila 1969), whereas in central Europe most beetles overwinter underneath the bark of standing or lying trees (Faccoli 2002). Wermelinger and Seifert (1999) argue that survival of larvae and pupae during winter is possible, but *I. typographus* only hibernates as adult in Fennoscandia (Christiansen and Bakke 1988). Winter mortality for beetles hibernating in the bark was roughly 50% when they experienced -10°C (Faccoli 2002). Butovitsch (1941) also calculated the winter mortality to ~50 % during a mass propagation of *I. typographus* after a storm felling in northern Uppland, Sweden, December 1931. The cold hardiness of *I. typographus* during different developmental stages was studied by Annila (1969) who found that the super-cooling of larvae was -12 to -14°C, the pupae survived slightly lower temperatures and the adults were all dead at -32°C. If the beetles were starved they survived lower temperatures better than if they were newly fed (Annila 1969). The diapause of *I. typographus* in central Europe is probably terminated in December/January and the beetles then remain inactive until the temperature rises above a threshold for activity (Doležal and Sehnal 2007).

Weather effects on host resistance

Weather phenomena such as heat and drought can affect the host tree negatively and are considered to predispose the trees to attack and aggravate bark beetle epidemics (Christiansen and Bakke 1988). Though, direct effects of spring weather are mostly, apart from rare cases of extreme drought, a more important factor affecting *I. typographus* dynamics than indirect effects working through the host tree (Christiansen and Bakke 1997). As a response to the selective pressure from bark beetles, their associated fungi and other pests and diseases, coniferous trees have evolved mainly two basic types of defense mechanisms, i.e. the constitutive defense and the induced defense (Christiansen et al. 1987; Franceschi et al. 2005). The constitutive defense system includes chemicals (e.g. terpenoids and phenolics) stored in the phloem and wood and is formed by anatomical structures (resin-ducts) existing in the tree. It forms a front line of defense to potential invaders by combining chemical toxicity and physical barriers (Franceschi et al.

2005; Zhao 2011). When bark beetles bore through the bark, the beetles may be haltered by the primary defense (Franceschi et al. 2005). Around each attack point the induced defense system is activated by hypersensitive wound reactions, traumatic resin ducts are formed and mass defensive compounds are produced (Franceschi et al. 2005). This overlapping defense structure provides the conifers with powerful protection against a wide range of organism that may attack the tree. Still, certain organisms such as bark beetles have evolved strategies to overcome- or to avoid these defenses (Franceschi et al. 2005). As was mentioned before these consist of pheromonal communication, association with blue-stain fungi and tolerance for host resins.

For *I. typographus* blown-down trees or standing weakened tress is main host material as healthy trees normally are resistant to beetle attack (Christiansen and Bakke 1988). Reduced tree vigor in Norway spruce can have various reasons such as long term or imminent water stress (Worrell 1983), damaged fine roots caused by swaying trees affecting the water uptake (Christiansen and Bakke 1988), or when planted out of its natural range (e.g. in the lowlands of central Europe) (Otto 1985). In contradiction, storm damaged trees (e.g. leaning stems) have showed an increased (induced) resistance to mass inoculation of a virulent blue stain fungi, *Ceratocystis polonica* associated with *I. typographus* (Zhao et al. 2011). It is hypothesized that changes in terpene and phenolic composition is at least partly responsible for the induced resistance.

A theoretical model (Fig. 1) formulated by Berryman (Berryman 1978; Berryman 1982) is linking the threshold of successful beetle attack to the resistance of individual host trees or stands and determines the number of beetles needed to overcome the defense of the tree. The model shows that successful colonization of living trees is possible only at high beetle population and/or reduced resistance, and subsequently the situation will change from endemic (non-outbreak) to epidemic (outbreak). The modeled assumptions are supported by empirical studies (Larsson et al. 1983; Mulock and Christiansen 1986; Christiansen and Glosli 1996).

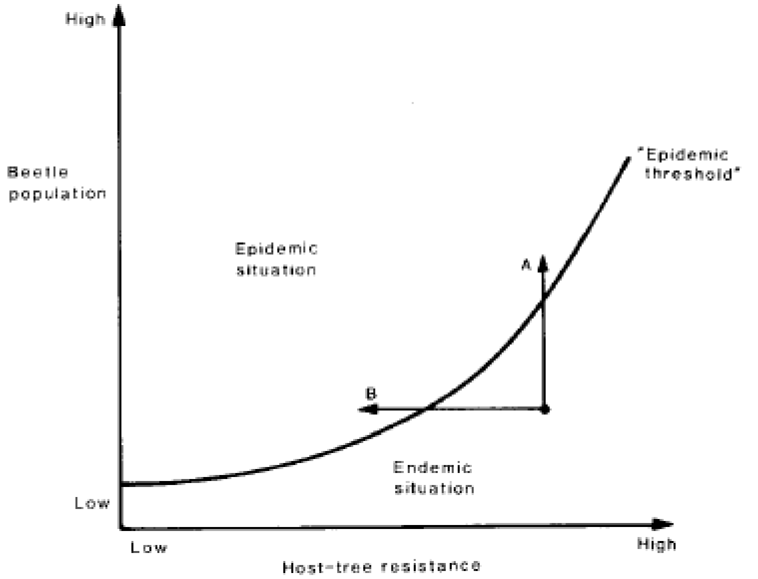

Figure 1. A theoretical model for the relationship between host-tree resistance and threshold of successful bark beetle attack, after Berryman (1978; 1982).

One example of an *I. typographus* outbreak that was triggered by drought (i.e. reduced host-tree resistance) occurred in Norway in the 1970s. The outbreak began after the extensive storm damage in 1969 and was extending in area and increasing in intensity after several dry summers (1974-1976) (Bakke 1983). The attacks were most frequent and severe in areas with permian geological formations predisposed to drought due to fissuring in the bedrock, large continuous spruce forest, other severely drought affected sites, valley sides especially south and west facing, higher site class and in lower altitudes (0-400 m.a.s.l) (Worrell 1983). In addition to the drought of 1974-1976, the entire period 1969-1980 showed a rainfall deficit equal to a normal one year precipitation (Worrell 1983). Similarly, the exceptionally warm and dry summer 2006 resulted in substantial tree mortality probably as a result of both high flight activity and reduced tree vigor (Långström et al. 2009).

Climate change scenarios and *Ips typographus*

Both mean temperature and the frequency of storms and other extreme weather events such as heat spell, dry spell and flooding is likely to increase in the future. That is the general conclusion from assessments made by the intergovernmental panel on climate change (IPCC) (Cubasch et al. 2001). Though, for northern Europe there is so far no consistent observational evidence for any persistent trend in storm frequencies (Heino et al. 1999), actually for the last 200 years the number of storms in Scandinavia has been remarkably stable with no systematic change (Bärring and von Storch 2004). Anyhow a climate model by Benestad (2005) indicates increased storm frequencies and increased frequency of windthrows in the future in Europe, which also holds for Sweden (Fig. 2) and the rest of northern Europe during the late 20th century. In Sweden the pattern of total storm damages, largely coincides with the average wind distribution, with most damage done by winds from NW to SW (Nilsson et al. 2004). Besides possible changes in wind climate there are, however, other explanations such as a change in land use towards more productive forests, forest management efficiency by clear-felling, artificial regeneration followed by thinning, and subsequent changes in root architecture (Nilsson et al. 2004). Also, frozen soil conditions anchoring stands will be less common in a future warmer climate. Thus, trees will be more susceptible to windthrow (Schlyter et al. 2006).

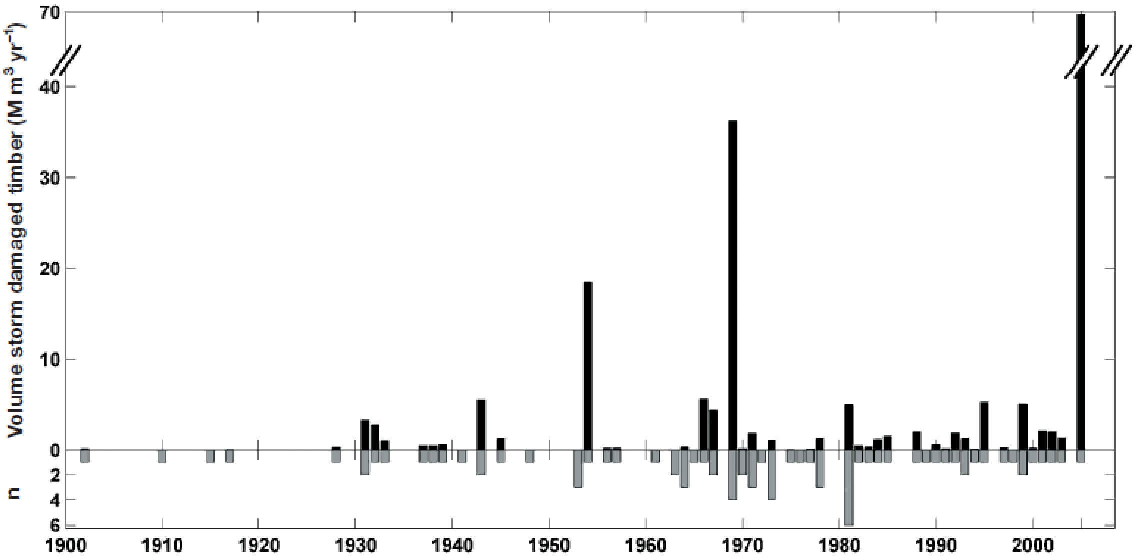

Figure 2. Annual total numbers of storms (grey bars) and annual damaged volume of timber in million m^3 standing volume (black bars) in Sweden, from Schlyter et al. (2006).

The effect of climate change has recently been reviewed regarding insects in general (Robinet and Roques 2010), for forest pests (Logan et al. 2003) and for bark beetles in particular (Heliövaara and Peltonen 1999). Models using different climate change scenarios have been used to predict future development and voltinism of *I. typographus* (Lange et al. 2006; Jönsson et al. 2007; Jönsson et al. 2009; Jönsson and Bärring 2010) leading to the conclusion that a warmer climate will allow increased voltinism and thus increased frequency of *I. typographus* outbreaks.

A warmer climate will lead to earlier spring swarming, and a faster development from egg to adult bark beetle will increase the probability of a second swarming period during the summer. Jönsson et al. (2007) modeled the temperature dependent population dynamics of *I. typographus* and evaluated the effect of regional climate change scenarios for the period of 2070-2099. With an increase in annual mean temperature of 2-3°C a second swarming will be the rule. However, with an increase below 5-6°C a development of a second generation will not be fulfilled. Model calculations by Jönsson et al. (2009) suggests that *I. typographus* in southern Sweden will be able to initiate a second generation in 50% of the years around the mid century and in 63-81% of the years by the end of the century. However, a second flight period of the new generation beetles is already occurring in southern Sweden. In all years since 2005-2011 callow beetles showed up in traps around the beginning of July (Öhrn 2009). A regional climate scenario model estimated the northward spread of bivoltinism in *I. typographus* and predicts southern Norway to be almost strictly bivoltine in 2071-2100 (Lange et al. 2006). It has been indicated that diapause may determine how far bi- and trivoltinism will expand in a warmer climate, as day length cues can restrict the length of swarming during the late summer (Jönsson et al. 2011). Further, Jönsson and Bärring (2010) conclude that there is a risk for amplification of otherwise modest bias climate model data in describing biological processes by accumulation of temperature (dd) and responses induced after crossing a discrete temperature threshold.

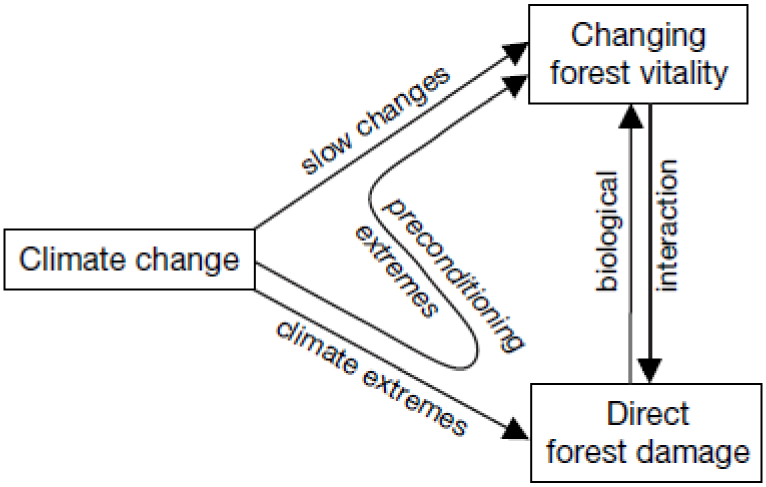

Figure 3. Conceptual model of impacts of climate extremes and raised mean temperature on forest vitality, after Schlyter et al. (2006).

When examining factors that affect Norway spruce vitality and its susceptibility to windthrow or vulnerability to bark beetle colonization it has been noted that modeled future climate is likely to negatively affect Norway spruce both directly (e.g. storm-fellings and indirectly (i.e. reduced vigour?) (Fig. 3) (Schlyter et al. (2006). Tree vitality is negatively affected by preconditioning extremes. The Norway spruce has very superficial root system that makes it more sensitive to drought. Thinned mature forest, exposed to high wind speeds, making the trees sway, will damage the fine roots (that are important for the water uptake) and predispose the tree for insect pests (Nielsen 2004). Schlyter et al. (2006) predicts the risk of summer drought conditions to increase for large parts of Europe north of the Alps in a future climate (year 2070-2099) and also with earlier start of the vegetation period there will be an increased risk for spring temperature backlashes. This risk will be higher in the southern parts of Sweden. In central Europe Norway spruce is often grown outside its natural geographical range. Bark beetles are predicted to do greater damage to Norway spruce that has been planted out of its native range on soils rich in N, P and K in the lowlands of Slovenia in a future climate (Ogris and Jurc 2010). Also, a climate driven model predicts the damage levels of *I. typographus* in Austria to be more than three times higher in 2099 than in 1990-2004 and a substantial time-lag between the start of adaptation measures and a decrease in damage

(Seidl et al. 2009). Kauserud et al. (2011) predict that due to the strong endogenous feedbacks of bark beetle systems that make them sensitive to perturbations such as climate change, these species may respond quickly to ecological changes such as decreased host defenses following changes in climate or forestry. On the other hand, higher temperatures may also benefit thermophilous parasitoids of bark beetles making them more active and aggressive (Heliövaara and Peltonen 1999).

Discussion and conclusions

The spruce bark beetle is an integral part of the boreal ecosystem, and bark beetle outbreaks belong to the natural dynamic of this system. They seem, however, to have increased during the last century both in Sweden and elsewhere, probably as a result of changed forest management. Now climate changes are predicted to significantly affect the frequency and severity of disturbances on the forest ecosystems (Bentz et al. 2010). In North America the mountain pine beetle *Dendroctonus ponderosae* has killed hundreds of millions of cubic meter of pine trees in recent years (Kärvemo and Schroeder 2010). The beetle is advancing in latitude and altitude to naïve host trees where they have been shown to have a higher reproduction (Cudmore et al. 2010). In Europe, *I. typographus* bivoltinism is already advancing in altitude (Forster and Meier 2009) and a northward movement is predicted in the future (Lange et al. 2006).

Temperature seems to be most crucial in controlling insect life in the north. Regarding bark beetles in general and *I. typographus* in particular, performance in trees is likely to be improved due to climate change. Higher temperatures and drought may have a synergistic negative effect on the spruce forest as water shortage weakens the host defense and an increased temperature will promote earlier flight in spring, faster preimaginal development. This will, additionally promote a second flight period in July, when, in addition, trees may be less resistant (Lange et al. 2006).

Increased temperatures in early spring (allowing first flight in mid April compare to mid May) could be more crucial for the bivoltinistic potential than increased temperatures during the end of the vegetation period due to limited day length, at least in the absence of evolutionary change in the responses to photoperiodic cues that mediate diapause induction. This has also been hypothesized for other insects, e.g. the grape berry moth *Paralobesia viteana* (Tobin et al. 2008).

Monitoring the development of concealed insects like phloem feeding bark beetles is problematic due to high variation in microclimatic conditions under the bark; especially the effect of solar irradiation can alter the temperature in the bark in exposed positions compared to the ambient temperature. Thus, field studies give higher variation in data than laboratory studies. When comparing laboratory experimental results (Wermelinger and Seifert 1998) with results of field studies (Annila 1969; Harding and Ravn 1985) thermal sums of different development stages differ; the thermal sums accumulated in field (in the air) is less than 75% of the thermal sums from laboratory for the whole development until the mature beetle emerge (Table 1). One possible explanation for this is effect of solar irradiation. The difference between the accumulation of heat under bark and the accumulation in the air is increasing with the amount of sunshine during the season (Coeln et al. 1996).

There are predictions of more stormy weather, but no increased storm frequency has been seen yet, and more storm damage has occurred in recent years (Nilsson et al. 2004), so in case of increased severity of storms we may see even more damages such as large stormfellings serving breeding material for bark beetles. We can also expect higher populations of *I. typographus* doing more damage to a maybe less defensive host tree in a future warmer climate. It seems to me as if size is more important than frequency since it is only after large stormfellings that we don't have the capacity to take care of all the storm felled trees before they are colonized by the beetles.

For a future climate forest management has to be planned and adapted for increased wind damages, severe drought and higher population levels of bark beetles.

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