In natural spruce stands, a change of generation is usually initiated by wind or bark beetle disturbances. We combined semi-temporary monitoring plots, remote sensing, and GIS in order to understand and model these processes. Sub-plots, called “active”, were located in areas with a high probability of bark beetle or wind disturbances. The optimal location of these plots is usually at an active forest edge, i.e., the zone of maximal change in bark beetle abundance over time, corresponding to the border between wind-damaged or bark-beetle attacked parts and undisturbed parts of a forest stand. The key variable investigated was tree mortality caused by bark beetles. Other variables were similar to those recorded in traditional forest monitoring. Tree defense indicators (resin flow, phenolic compounds) and reaction of a tree to bark beetle inoculation were measured. Terrestrial data were then combined with remote sensing data. Time series of satellite images were analyzed in order to define the pattern of wind and bark beetle damages. Weather monitoring data were used for predicting bark beetle and water stress development. All of the information was integrated in a GIS-based system and future bark beetle infestations were predicted. In this paper, we review previous studies and conclude that: (1) the hypotheses of habitat selection (non-host volatiles and semiochemical diversity) and location of moderately-stressed host trees are confirmed, although further work about olfactory orientation and host resistance is needed; (2) reactions of trees to bark beetle attack can be predicted by monitoring several parameters, e.g., air temperature and tree physiology; (3) data from ground monitoring can be integrated with GIS and remote sensing systems for bark beetle prognosis and management at the habitat and landscape levels.

Keywords: Spruce, Ips typographus, Attack, Drought, Host

Introduction

The most important processes of forest stand development are growth and disturbance (Stage 1973). Due to the effect of climatic changes, the role of disturbances is becoming more important (Kurz et al. 2008, Van Mantgem et al. 2009). Storms, drought and warm periods, together with temperature breaks in early spring, are very negative factors for Norway spruce forests, in particular allochthonous populations (e.g., Manion 1981). These events will be more frequent according to most of climate change scenarios. The important natural disturbances in spruce stands are wind and beetles. A significant part of European spruce forests is old with frequent disturbances. A change of generation is usually initiated by wind or bark beetles. The process of decline of an old stand may be relatively fast (Hlášny & Turčán 2009). Unfortunately, traditional forest monitoring plots (ICP - Forest level I or National Forest Inventories) focus on mature, managed stands in areas with no disturbances. These types of plots are selected according to their position in a net (e.g., 7 x 7 km square net). Only few plots are situated in remnants of semi-natural forests, where the consequences of natural disturbances are not solved by forest management.

The main aim of our research was to understand the mechanisms of Ips typographus attack on standing spruce, from habitat and host location to host acceptance (Schlyter & Biggins 1999). There are two main hypotheses for host location: random landing (Byers 1996), and primary attraction (Gries et al. 1989). Both methods of host location can be seen as subsequent steps after habitat (stand) selection, a behavior which is likely a balance of a positive input from the host (conifer) kairomone and a negative input from non-host (angiosperm broad-leaves) volatiles, or NHV (Zhang & Schlyter 2004). Such “semiochemical diversity” at the habitat level (Zhang & Schlyter 2003) may affect both herbivores and predators (Zhang & Schlyter 2010). Host acceptance is connected with host recognition, resistance and suitability (Raffa et al. 2008), which in turn are connected to tree health (Christiansen et al. 1987) and ecophysiology (Nelson & Lewis 2008).

Führer et al. (1997) demonstrated that attacks of Ips typographus occur on vigorously growing trees suffering from a sudden stress. This may be explained by a lack of constitutive defensive fast growing trees, combined with a stress-induced failure in the induction of secondary defense mechanisms. In endemic conditions, Ips typographus attacks downed trees on sun-exposed slopes with open canopy (Jakůš 1995). According to Raffa et al. (2008), the tree-killing bark beetle species display flexible host-selection strategies. When the populations are low, avoiding healthy trees is an adaptive mechanism. Vigorous trees pose a risk to beetles.

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Ips typographus attack regardless of the gradation phase and stand conditions (Jakuš et al. 2003b, Grozdki et al. 2006, Akkuzu et al. 2009). This indicates that questions of sun radiation and shading are important for understanding the mechanisms of I. typographus host selection.

The working hypothesis in the case of standing trees is that the I. typographus pioneer male locates and/or accepts the most susceptible host spruce trees (Moravec et al. 2002). The process of attack is initialized by a disturbance, such as wind throw or bark beetle related mortality, which usually results in removal of neighboring trees or their foliage. The remaining trees are suddenly exposed to direct solar radiation. In the case of dense stands with short tree crowns, large parts of the stem will in turn be exposed to the sun, increasing transpiration and water stress. Resistance of a tree to bark beetle would then be diminished. Higher temperatures on the sun-exposed bark would increase emission of bark beetle primary attractants (Baier & Bader 1997). The question of host resistance at a different scale is thus important. At the scale of an individual tree, tree physiology (Nelson & Lewis 2008) and secondar chemistry are likely the most important factors addressing host resistance (Urbanek Krajnc et al. 2010, Zhao et al. 2010). At the scale of habitats and landscapes, GIS-based modeling may help in understanding bark beetle damage.

The aim of this paper is to summarize the main results of our previous work on this issue and synthesize the progress of knowledge.

**Ground-level research and study plots**

We developed a semi-temporary monitoring pair plots approach to understand and model processes of bark beetle-caused spruce mortality at the forest stand scale. Generally, the active plots were located in areas with a high probability of bark beetle or wind caused disturbances, because of proximity to wind destroyed or bark beetle attacked areas. The control plots were situated in undisturbed forest stands (< 50 m from the active plots).

**Project Tatry (1999-2001)**

The project “Integrated risk assessment and new pest management technology in ecosystems affected by forest decline and bark beetle outbreaks (TATRY)” was conducted in natural spruce forests affected by bark beetle in the Tatra Mountains (Schlyter 2001, Grozdki et al. 2006, 2010).

**Plot design**

An altitudinal transect was established including 5 pairs of monitoring plots, located between 1000 and 1400 m a.s.l. at a 100 m altitude interval. Each pair consisted of one active plot (60 trees) on the stand edge or bark beetle spot, and one control plot (30 trees) within the forest stand. The plots were visited several times a year in order to identify trees that were attacked by bark beetles (Grozdki et al. 2003). The measured or monitored variables are shown in Tab. 1. In addition, beetle chemoception of trees and habitat was studied in the field and laboratory (Zhang & Schlyter 2004).

**Main results**

Main results reported here are from Schlyter (2001). (1) Relatively healthy trees, i.e., recovering after a damage, with high defoliation of the primary crown and high percentage of secondary shoots, were more susceptible to beetle attack than those with a low defoliation of the primary crown and a low percentage of secondary shoots (Polák et al. 2007). (2) Phenolic predictors of tree resistance against fungal attacks were also good predictors for tree resistance against bark beetle attacks in the field (Lieutier et al. 2003). Three such phenolic predictors (catechin, taxifolin, and resveratrol) were shown to be anti-feeding semiochemicals for bark...
beetle (Faccoli & Schlyter 2007), thus affecting host acceptance. (3) A model for bark beetle development in relation to temperature was developed and tested (Netherer & Pennerstorfer 2001, Netherer & Noppmayr 2003). (4) Little information about NHV blends was used for forest protection in the field (Jakuš et al. 2003b).

Project Spiš (2003-2006)

The project “Analysis of causes and possible measures against mass die-back of spruce stands in border regions of north Slovakia” was conducted in planted spruce forests affected by chronic decline and bark beetle attacks (Jakuš 2001).

Plot design

An altitudinal transect was established, including 3 pairs of monitoring plots located between 740 and 1100 m a.s.l. Each pair consisted of one active plot (30 trees) on the stand edge or bark beetle spot in the forest and one control plot (30 trees) within the forest stand. The plots were visited several times a year in order to identify trees that were attacked by bark beetles. The measured or monitored variables are shown in Tab. 1.

Main results

Main reported here are from Jakuš (2006). Trunk cooling by transpiration flow is an important mechanism of tree protection against overheating. Our results showed differences in the cooling abilities of sun-exposed parts on sunny days. The level of overheating was higher in trees attacked by bark beetles than healthy trees, because higher defoliation leads to slower transpiration flow.

Project Kysuce (2005-2008)

The project was carried out in planted spruce forests affected by chronic decline and bark beetle attacks.

Plot design

Two mini plots were established, each consisting of three spruce trees. In one plot, drought stress was simulated using a shelter to prevent root access to precipitation. The second plot was used as a control. Sap flow, stem circumference and soil water potential were measured. Air temperature, air relative humidity, global radiation, and precipitation were measured in an open area. Bark beetle boring abilities were tested on the monitored trees (Turčáni & Nakládal 2007). The measured or monitored variables are shown in Tab. 1.

Main results

Only slight differences in sap flow rates between the plots were recorded, suggesting that only small differences in soil water regime can be achieved by sheltering precipitation to the tree roots. As a result, the bark beetle boring responses were also unclear (Turčáni & Nakládal 2007).

Project Kyrrl (2008-2011)

The project “Study and optimization of real efficiency of control measures against Ips typographus in various gradation phases” investigated the role of drought as a main driving factor of bark beetle outbreaks (Zajickova & Matousek 2010).

Plot design

Two large-scale research areas were established. A large roof at 2 m above the ground level and isolation of the root system from side ground water inflow controlled the water regime. Different physiological reactions of the drought stressed trees can be induced by decreasing soil water potential. The first research area “Brdy” was located at 650 m a.s.l., with 6 drought-stressed trees and 12 control trees. Tree response to drought was monitored by dendrometers and soil water potential sensors. A manipulation experiment with adult male beetles, testing the willingness of males to enter the phloem and create a nuptial chamber, was performed in 2008 and 2009. There are two critical factors for such experiments: (i) a large number of male beetles in good health and (ii) suitable weather conditions at the time of the experiment. The second research area “Kostelec” was located at 350 m a.s.l. in a Norway spruce monoculture, with two drought-stressed and two control plots (25 m x 25 m). Physiology of four trees was monitored by dendrometers and sampling needles for proline analysis. The “Kostelec” experiment began in 2010.

Main results

Main results reported here are from Zajickova & Matousek (2010). (1) Trees exposed to enhanced drought did not show any resin flow when conducting the manipulation experiment with male beetles at the beginning of an enhanced drought in 2008. In 2009, the response level of the defense system of the tree was higher, and flow of resin was recorded in each nuptial chamber. We concluded that the level of drought stress affects pest resistance of the tree. (2) During dry periods, drought-stressed trees showed no changes in stem circumference, while they showed the same values of stem diameter change as control trees during rainy periods.

Remote sensing and GIS based research

Project Tatry (1999-2001)

Methods

Vegetation change analysis, digital elevation model, and stand characteristics were integrated in the remote sensing part of this study. Time series of LANDSAT images were used in this study (Jakuš et al. 2003a).

Main results

Main results reported here are from Jakuš et al. (2003a). The spatial pattern of the spread of bark beetle outbreaks was related to the phase of the outbreak and insolation (incoming solar radiation). Progression of the attacks arose mainly from initiation of new bark beetle spots. In the culmination and retrogradation phases, outbreaks spread by further expansion from old spots. The spots spread in all directions except south (forest edge oriented to north). We recorded a time-dependence in the decrease of distances between old and new spots. In the first stage of the outbreak, the beetles migrated over fairly long distances. At later stages, the available resources were more limited, thus the beetles were more likely to attack resources adjacent to old spots even though they were less suitable.

Project SLOVABBO (2003-2004)

The results of project Tatry were used for developing a first version of a GIS and remote sensing based early warning system for bark beetle infestations (Kissiyar et al. 2005). The results were used in the TANABBO model (Tatra National Park Bark Beetle Outbreak - the name of the model is different from the project acronym).

Methods and main results

Main results reported here are from Jakuš et al. (2005) and Kissiyar et al. (2005). A rating system for assessing the predisposition of forests to bark beetle attack was developed on the basis of known causal relationships between bark beetle outbreak and environmental parameters. A system of sub models was used. Each sub model produced a certain output that was then used in the model. A one-year prognosis of bark beetle attack was based on modeling of the two processes connected with the spread of a bark beetle outbreak: spot initialization and spot spreading (Jakuš et al. 2003a). The actual risk of beetle attack was estimated by means of a bark beetle development model (Netherer & Pennerstorfer 2001, Baier et al. 2007), i.e., a vegetation health model derived from MODIS satellite images and a drought index based on soil characteristics, precipitation data, and potential evapotranspiration.

Discussion

Semi-temporary monitoring pair plots

The approach of semi-temporary monitoring pair plots was used in several studies and was helpful in investigating the mechanisms of I. typographus attack on spruce. The combination of traditional monitoring techniques and high resolution remote sensing data is very useful for research purposes.
plots with semi-temporary monitoring pair plots helped to better understand the mecha-
nism of bark beetle related disturbances. Results showed that I. typographus mostly
attacks moderately stressed, "resilient" trees sensu Polák et al. (2007). The whole se-
quence of mechanisms is still unclear, in par-
ticular about host location and attack (habitat
location, host location, host acceptance,
overcoming of defences). Interestingly, while
no "primary attraction" sensu strictu (Ander-
son 1948) has been proven, the sensory array
of I. typographus includes many receptors
for host monoterpenes (Andersson et al.
2009, Andersson et al. 2010). The defense at
tree and stand scales may be explained by
water stress (project Kyrill).

Tree thermal properties and water stress
Hais & Kučera (2008) showed that surface
temperature in a spruce forest is strongly in-
fluenced by topography; slope and aspect in-
fluence potential radiation and heat load.
Higher surface temperatures can be expected
at forest edges during clear sky conditions in
summer. Part of the I. typographus attack
mechanism is connected with the effects of
solar radiation and surface temperatures on
individual trees (projectSpiš) and forest
stands (Jakůk et al. 2003B, Grodzki et al.
2006, Akkuzu et al. 2009). This is also in
agreement with Schopf & Köhler (1995).

Drought predisposes spruce to bark beetle
attack. Questions related to water stress were
studied in projects Spiš and Kysuce in
mountain conditions. We did not obtain clear
data due to the variability of the na-
tural conditions. In contrast, project Kyrill
provided evidence in support of the role of
water stress in predisposing spruce to I. ty-
pographus attack.

Thermal sensing is a proxy of insolation
and water stress effects on trees. According
to Jones & Schofield (2008), it is primarily
used to study plant water relations and spe-
cifically stomatal conductance, because a
major determinant of leaf temperature is the
rate of evaporation or transpiration from the
leaf. The cooling effect of transpiration
arises because a substantial amount of
energy is required to convert liquid water to
water vapor.

Tree health and host resistance
The results of project Tatyro also showed
the importance of parameters related to
spruce crown transformation and host resis-
tance, in accordance with Moravec et al.
(2002). Malenovsky et al. (2008) suggested the
use of remote sensing for mapping crown
transformation. One type of markers of
spruce host resistance are phenolic com-
 pounds (Brigolinos et al. 1998), which may
affect host colonization (Schlyter 2001) and
are active as antifeedant semiochemicals
(Faccoli & Schlyter 2007). According to
Sokoupová et al. (2001), it is possible to as-
sess the content of phenolic compounds in
spruce needles with the use of remote sen-
sing techniques.

Key variables
Our research suggests that several variables
related to I. typographus attack can be mea-
sured in ground plots and used for modeling
bark beetle disturbances via GIS. The main
variables are indicators of water stress (sap
flow, stem diameter) and the surface tempe-
rature of trees or stands. In addition, crown
transformation and phenolic content are also
recommended as possible variables to be
measured.

Practical applications
The knowledge gained during project Tatry
on the anti-attractant and semiochemical di-
versity effects of NHV (Zhang & Schlyl-
ter 2003, 2004) is now being put into practice
for forest protection (Jakúš et al. 2003B, Jac-
tel et al. 2011, Schiebe et al. 2011). The re-
sults from GIS and remote sensing applica-
tion were used for decision making in NP
Tatry (Schlyter 2001, Grodzki et al. 2006) and
NP Sumava (Turčáni et al. 2008).

Conclusions
1. Our observations and experiments confir-
med the hypotheses of habitat selection
(non-host volatiles and semiochemical di-
versity) and location of moderately-stress-
  ed host trees, although further work about
  olfactory orientation (to habitat cues and
  host odor) and host resistance is needed.

2. Reactions of trees to bark beetle attack can
be predicted by monitoring several para-
meters, e.g., air temperature and tree phy-
siology.

3. Data from ground monitoring can be in-
gerated with GIS and remote sensing sys-
tems for bark beetle prognosis and mana-
gement at the habitat and landscape levels.

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