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Assesment of Ips typographus attacks in relation to site and stand characteristics in managed and unmanaged oriental spruce (Picea orientalis (L.) Link) stands

İşletilen ve işletilmeyen doğu ladini (Picea orientalis (L.) Link) meşcerelerindeki Ips typhographus L. saldırılarının yetişme ortamı ve meşcere özelliklerine göre değerlendirilmesi



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Abstract

This study aimed at investigating the effectiveness of management practices for reducing the negative impacts of Ips typographus L. on Oriental spruce (Picea orientalis (L.) Link.) forests, and to review the best site factor(s) associated with Ips typographus infestation. Two sites, Hatila Valley National Park (HVNP-unmanaged site) and Saçinka Forest Sub-District Directorate (SFSD-managed site) were chosen to compare the stand characteristics (mean age, height, bark thickness, basal area, stand density and tree diameter) and soil properties (pH, organic matter-OM, soil texture, and nutrients). At both sites, the sampling plots were taken from the north and south-slope aspects (NSA and SSA) and from upper and lower-slope positions (USP and LSP) on each site. In general, the results showed that in HVNP, Picea orientalis stands had higher stand age, bark thickness, basal area, and tree diameter, but lower soil pH, OM, nutrients, percent clay and silt content than those in SFSD. Among the stand characteristics, the stand age was positively correlated (r = 0.916) to the mortality rates in HVNP. Besides, Picea orientalis stands on SSA and at USP were more damaged than on NSA and at LSP. In conclusion, the results indicate that forest management practices including thinning, pruning, and cleaning can have a significant favorable influence on Picea orientalis forests to minimize the risk of Ips typographus attacks.

Bu çalışma, Doğu Ladini (Picea orientalis (L.) Link.) ormanlarındaki Ips typographus (L.) saldırısının olumsuz etkilerini azaltmada ormancılık uygulama faaliyetlerinin etkisini ve Ips typographus'un saldırısıyla ilişkili en etkili yetişme ortamı faktörlerini belirlemeyi amaçlamıştır. Çalışma alanları olarak Hatila Vadisi Milli Parkı (HVNP-işletilmeyen) ve Saçinka Orman İşletme Şefliği (SFSD-işletilen) seçilmiş ve meşcere karakteristikleri (yaş, boy, kabuk kalınlığı, sıklık, çap, kapalılık) ile toprak özellikleri (pH, organik madde-OM, tekstür ve besin elementleri) karşılaştırılmıştır. Her iki çalışma alanında, deneme parselleri, kuzey ve güney yamaçlar ile bu yamaçların üst ve alt rakımlarından alınmıştır. Genel olarak sonuçlar, HVMP alanındaki Picea orientalis meşcerelerine ilişkin yaş, kabuk kalınlığı, göğüs yüzeyi ve çapın SFSD alanındaki meşcerelerden daha yüksek, toprak pH, OM, besin elementleri, yüzde kil ve toz miktarı bakımından ise daha düşük olduğunu göstermiştir. HVNP alanında, meşcere özelliklerinden meşcere yaşı ile ağaç ölüm oranları arasında pozitif yönde anlamlı bir ilişki (r = 0.916) belirlenmiştir. Bunlara ek olarak, güney bakan meşcereler ile üst rakımlardaki meşcerelerin, kuzey bakan ve alt rakımlardaki meşcerelere göre daha fazla Ips typographus saldırısına maruz kaldığı tespit edilmiştir. Sonuç olarak, bulgular, aralama, budama ve örtü temizliği gibi ormancılık işletme faaliyetlerinin, Ips typographus'un Picea orientalis ormanlarına saldırı riskini azaltmada pozitif yönde önemli bir etkiye sahip olabileceğini göstermektedir.

INTRODUCTION

The eight-spined spruce bark beetle, Ips typographus is one of the most dangerous forest pests on Picea abies in Europe (Wermelinger 2004) and also on Picea orientalis in Turkey (Akkuzu et al. 2009, Sariyildiz et al. 2008). In Central and Eastern Europe, lots of money, effort and time were spent to understand the dynamics of outbreak events, tree and stand susceptibility to bark beetle attacks, and the factors that predispose forest stands to higher mortality in pure Picea abies forests (Dutilleul et al. 2000, Sproull et al. 2015). In those studies, the intensity of Ips typographus attack on Picea abies has been shown to vary greatly with topography (aspect and slope position), stand structure, and environmental factors or combination of those factors (Kautz et al. 2013, Mezei et al. 2014). It has been stated that south-exposed and sunlit trees are preferably attacked by *Ips typographus* (Jakuš et al. 2011ab). Stand density, basal area or stand density index, tree diameter, and host density are consistently identified as primary attributes associated with bark beetle infestations (Jactel et al. 2012). Wermelinger (2004) reported that higher proportions of spruce trees in a stand enhanced *Ips typographus* attacks as did trees older than 70 years, with trees over 100 years being most susceptible. On the other hand, multiple regression analyses by Dutilleul et al. (2000) has indicated that altitude and soil nutrients, such as N, P and Mg, can also have a significant influence on *Ips typographus* attack rates.

Many researchers and foresters agree that forest management practices, including regular thinning and relatively short rotation cycles, decrease forest susceptibility and vulnerability to bark beetle outbreaks (e.g. Christiansen and Bakke 1988, Jactel et al. 2012). Stand density reduction can improve stand growth and enhance forest health in the long term (Sohn et al. 2013). While measures to prevent bark beetle attacks are taken as a matter of course in managed forests, the protected forest areas and national parks are considered by many people as a natural habitat for bark beetles (Valeria et al. 2016). Nature conservationists and some researchers even argue that the pest population may have an opportunity to increase with intensive management activities (Schowalter and Filip 1993). Some certain primary scolytids such as Ips typographus can have more favorable microclimate conditions under the thinned stands (Väisänen et al. 1993).

These contradictive arguments have become the subject of the present study, which aimed to investigate the stand and soil characteristics of managed and unmanaged *Picea orientalis* concerning *Ips typographus* (L.) attack. Despite intense research on the susceptibility of *Picea abies* stands to *Ips typographus* attack, statistical relationships between infestation intensity and site characteristics of *Picea orientalis* stands have not yet been found. *Picea orientalis* is a native species to Turkey, covering about 350.000 ha of land (OGM, 2015). The first flight of *I. typographus* in the north-eastern Black sea region is

generally at the beginning of April at an average altitude of 700 m (Keskinalemdar et al. 1987). This first flight can extend until the end of May depending on climatic conditions and altitude. The shortest generation time under the laboratory conditions has been determined as 24 days in an average of 24 °C and 51% humidity. In the conditions of the land, this period was found to be 81 on average at 1550 m and 85 days on average at 1700 m (Keskinalemdar et al. 1987). It was reported that Ips typographus entered this province from the neighboring country, the Georgian Republic. Since then, the occurrence of the pest has spread to all Picea orientalis stands in northeast Turkey. Picea orientalis forests in the region grow under similar climate conditions and also show similarities in terms of aspect, elevation, slope angle, steepness, and relief. Silvicultural activities apply on pure Picea orientalis stands or a mixture with other tree species according to the management plans. However, Picea orientalis stands growing in National Parks are under protection, and silvicultural activities are not allowed under protected areas. Over the last three decades, it can be virtually seen that Ips typographus damage on the managed Picea orientalis stands are less than on the unmanaged Picea orientalis stands, even though those managed Picea orientalis stands are closer to the border of Georgian Republic. Topographical factors (mainly, slope aspect, slope angle, and elevation) in Artvin region are important features influencing microclimate, soil characteristics, plant species composition, ecosystem development, site productivity, litter decomposition, and nutrient cycling (Sariyildiz et al. 2005). In Hatila Valley National Park, it is noted that pure Picea orientalis stands on SSA (south slope aspect) and at USP (upper slope position) are preferably more infested by Ips typographus than on NSA (north slope aspect) and at LSP (lower slope position). This information is based on the salvage logging data obtained from Artvin Regional Forest Directorate.

The objective of this study was to compare the stand characteristics (stand age, height, bark thickness, basal area, density and tree diameter) and soil properties (soil pH, organic matter, texture, soil carbon and nutrient content) between the managed and unmanaged *Picea orientalis* stands, and to find the best site factor(s)

affecting the susceptibility of *Picea orientalis* stands by *Ips typographus*.

MATERIAL and METHODS

The study sites were chosen within the border of Saçinka Forest Sub-District Directorate (41° 13' 28" N, 41° 50' 25" E) (SFSD-managed forest site) and in the Hatila Valley National Park (41° 6' 25" N, 41° 39' 30" E) (HVNP-unmanaged, protected site) in Artvin Province, north-east Turkey (Figure 1). HVNP has been under protection since 1994, and silvicultural activities are not allowed in this site since then. The first major infestation by *Ips typographus*

was noted in 2000 in HVNP, but nothing was done as bark beetle damages were also considered a natural part of this national park. However, the intensity of *Ips typographus* attack became so severe that more than 20000 ha *Picea orientalis* stands in HVNP were infested by *Ips typographus*. Only management activity carried out by Artvin Regional Directorate of Forestry in the sites was to use pheromone traps. Other Forestry Operation Directorates where *Picea orientalis* grows pure or a mixture of other tree species carried out all silvicultural activities according to the management plans. Among these Operational Directorates, SFSD site was the other area of the present study as the managed site.

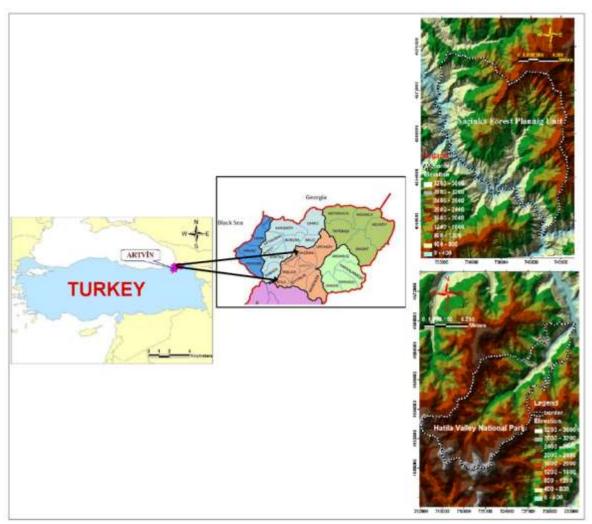


Figure 1. Location of the study area in Artvin, Turkey

SFSD is near the border of Georgian Republic and located in the north-eastern part of Artvin which is characterized by a dominantly steep and rough terrain with an average slope of 57% and an altitude vary from 185 to 2469 m

above sea level. The total area is 13314 ha. Dominant tree species are spruce (*Picea orientalis*), oriental beech (*Fagus orientalis*), oak (*Quercus petraea*), Scottish pine (*Pinus sylvestris*), Nordmann fir (*Abies nordmanniana*)

subsp. *nordmanniana*), hornbeam (*Carpinus betulus*) and alder (*Alnus glutinosa*).

HVNP is located in the south-western part (about 40 km away from the SFSD site). Mean slopes range from 30% to 70% in the mountainous region and the elevation can reach up to 2300 m. Total land is about 16988 ha. The vegetation type is considerably varied in the HVNP site. Dominant tree species in HVNP are semi-arid pseudomaquis forests (200-600 m), semi-humid *Quercus*-Pine forests (600-900 m), semi-humid *Picea-Fagus* forests (900-1300 m), humid *Picea-Fagus* forests (1300-1700 m), and humid *Picea-Fagus-Pinus* pure or mixture forests. Above altitudes of 1700 m up to 2200 m pure *Picea orientalis* stands are dominant at both the managed and unmanaged study sites.

The climate in Artvin Province is characterized as severe winters and hot summers (1980-2017 data from the meteorology station in Artvin). At the lower elevations (about 1700 m. a.s.l), the mean annual precipitation and temperature were 1392 mm and 16 °C, respectively, while at the upper elevations (about 2200 m. a.s.l), the mean annual precipitation and temperature were 1571 mm and 14 °C respectively.

The sampling plots (20 x 20 m²) were chosen from NSA (north slope aspect) and SSA (south slope aspect), and also USP (upper slope position) and LSP (lower slope position) on each slope aspect. The sample plots showing different mortality rates in HVNP (number of dead trees was each plot divided by the total number of trees in the plot) were named as; (1) highly attacked plots (over 50% tree mortality), (2) moderately attacked plots (25-50% tree mortality) and (3) slightly attacked plots (less than 25% tree mortality). This sampling design gave us total 36 plots in HVNP [2 slope aspect (North and South-exposed site) x 2 slope positions (top and bottom) x 3 replicates x 3 levels of attack (highly, moderately and slightly) = 36 sample plots]. The same number plots were also taken in SFSD without considering the levels of attack [2 aspects (north and south) x 2 slope positions (top and bottom) x 9 replicates = 36 sample plots].

At each plot, each tree (stem >8 cm diameter at breast weight) was measured for height, diameter, bark

thickness, and tree architecture were noted. The age of five mature and taller trees in each plot was also determined. Tree age was determined by counting each annual growth ring in the trunk of the tree. Blume-Leiss clinometer was used to measure the tree heights. Canopy cover was visually decided in each plot and then this determination was corrected by measurements of stem number and diameter at breast height. A diameter tape was used to measure the diameter at the breast height (DBH). After that, the basal area was calculated using the equation as follows; basal area = $pi \times (DBH^2/4)$, Where pi= 3.14, DBH = diameter at breast height. Mean stand basal area was determined by totaling the basal area of each tree in the plot, and dividing by the area of the plot. Stand density was calculated in each sample plot based on the numbers of standing and dead trees. Percent mortality (%) was calculated using the ratio of the dead tree numbers to all tree numbers within each plot. Bark thickness was calculated by subtracting the inside bark diameter from the outside bark diameter of a disk.

Mineral soil samples were collected from three soil depths of 0-15 cm, 15-35 cm and 35-65 cm. that were sampled in an area of $0.25 \, \text{m}^2$ ($0.5 \, \text{m} \times 0.5 \, \text{m}$) at a distance of 2 m from center trees. The stones, roots, and macrofauna in the field samples were removed by sieving (< 2 mm). They were then mixed to have one representative sample for each study site.

A glass calomel electrode was used to measure the soil pH in deionized H₂O. The soil texture was determined by the hydrometer method (Gülçur 1974). Percent of soil organic matter was found using the wet digestion method (Kalra and Maynard 1991). Soil Ca, Mg, Na, Fe, Zn, Cu and Mn were determined by atomic absorption spectrophotometer. Α flame emission spectrophotometer was used for K concentration, while a continuous flow calorimetry was used for P concentration according the method by Allen (1989). The analyses were done in triplicate.

Data analysis

The normality of *Picea orientalis* stand variable and soil data from SFSD and HVNP was tested using the Kolmogorov Smirnov test (Can 2018). The data checked

for normality showed a non-normally distribution and so the data was logarithm (log 10 (x + 1)) transformed or square root transformed to follow a normal distribution. The impacts of slope position and the elevation (slope position) on the stand variables for SFSD and HVNP were analyzed using two-way ANOVA. The effects of management activities, slope aspects (north and south), slope positions (upper and lower), and level of attack on percent mortality were compared for all data using Mann Whitney U Test (Can 2018). The relationships between the mortality and *Picea orientalis* stand variable data were analyzed using the Spearman rank test. All statistical analyses were carried out using IBM SPSS Statistics 20 for Windows.

RESULTS and DISCUSSION

The results in the present study showed that Ips typographus attack on Picea orientalis stands varied significantly between SFSD and HVNP (p<0.001), the slope positions (p<0.05) and the levels of attack (p<0.001) (Table 1). The intensity of Ips typographus attack on Picea orientalis stands varied significantly with the forest management practices. Percent mortality caused by Ips typographus attack on Picea orientalis was much higher in the unmanaged site (HVNP) than in the managed site (SFSD) (Table 2 and Table 3 respectively). The differences in crown conditions and tree distances combined with the differences in microclimate and light due to forest management activities, especially tree thinning between the managed and unmanaged sites could be responsible for the differences in percent mortality rates found in the present study.

Table 1. Changing of mortality rate (percent mortality) according to management, slope position, slope aspects and infestation severity using Mann Whitney U Test

		Median	Interquartile Range (IQR)	Р	
Managamant	Managed-SFSD	30	48.50	0.000	
Management	Unmanaged-HFNP	6	6.50	0.000	
Aspect	North	10	21.75	0.282	
	South	11	35.25	0.282	
Slope position	Тор	13	32.75	0.016	
	Bottom	9	20.25	0.016	
Infestation severity	Highly	72.5	34.0		
	Moderately	28.0	16.0	0.000	
	Slightly	7.0	7.65		

The effectiveness of forest management activities to minimize the risk of bark beetle attacks was widely studied and discussed by many researchers and foresters, who were strongly suggested for other bark beetles and coniferous tree species that active forest management was critical to maintaining healthy trees that were less susceptible to mountain pine beetle attack (Zausen et al. 2005, Fettig et al. 2007). Forest management activities, especially thinning to reduce intraspecific competition, thereby also reducing the stress level of a plant and increasing its access to water, nutrients, and light, is recommended by researchers (e.g. Wallin et al. 2004). Thinning can also allow higher photosynthetic rates with more carbohydrates being available for growth and defense. It is previously reported that several bark-beetle

species avoid thinned stands, which are typical for managed forest landscape (Peltonen et al. 1997). Many researchers showed that thinning redistributed growing space to desirable trees and reduced risks associated with fire, insects, and diseases (Smith 1986)

Jakuš et al. (2011a) stated that fostering the development of larger crowns through thinning could considerably increase stand resistance to bark beetle attack. Larger distances between trees could be achieved by thinning or planting at larger spacing. They also showed that surviving trees had different characteristics related to crown geometry, collective stand shading, trees spacing (distance factors), primary structure defoliation and height than neighboring dead trees.

Table 2. Some topographic features and stand characteristics according to slope position and slope aspects in Hatila Valley National Park (HVNP-unmanaged site).

Parameters		NSA (USP)			NSA (LSP)			SSA (USP)			SSA (LSP)		
	High	Moderate	Slight	High	Moderate	Slight	High	Moderate	Slight	Highly	Moderate	Slight	
Elevation (m)	2137	2141	2146	1823	1801	1769	2142	2131	2123	1862	1842	1808	
Slope angle (%)	38	48	47	45	40	38	43	42	43	62	68	65	
Canopy cover (%)	22	70	90	57	83	93	18	90	63	50	82	92	
Mortality (%)	87	30	16	56	26	5	95	23	44	70	28	10	
Age (yr)	130	108	85	118	102	89	140	125	110	123	108	97	
Height (m)	17	20	22	24	26	28	23	25	27	29	31	33	
Bark thickness (cm)	3.01	2.82	2.33	2.68	2.47	1.38	3.7	3.33	2.94	2.86	2.54	1.71	
Basal area (m²ha-1)	96	71	61	47	36	34	106	80	64	73	69	52	
Stand density	13.2	12.1	8.88	8.74	7.65	7.10	16.5	12.1	9.74	11.4	10.8	7.62	
Tree diameter (cm)	43	38	35	24	22	21	58	52	36	31	27	24	

Table 3. Some topographic features and stand characteristics according to slope position and slope aspects in Hatila Valley National Park (HVNP-unmanaged site).

	,											
Parameters		N	SA		NSA			SSA	4		SSA	
Parameters		(U	SP)		(LSP)			(US	P)		(LSP)	
Elevation (m)	2010	1994	1985	1750	1760	1810	1990	1983	1988	1830	1865	1875
Slope angle (%)	45	42	38	50	45	40	50	48	45	62	60	58
Canopy cover (%)	85	95	96	90	93	95	86	96	97	88	94	96
Mortality (%)	10	14	4	22	11	2	24	17	8	21	15	5
Age (yr)	83	79	75	87	86	81	85	75	80	88	86	86
Height (m)	26	28	30	28	27	35	26	30	35	36	34	34
Bark thickness (cm)	2.41	1.95	1.87	1.60	1.40	1.30	1.81	2.20	1.91	1.65	1.82	1.82
Basal area (m²ha-1)	57	50	55	42	39	32	53	49	55	45	46	46
Stand density	6.78	6.28	5.62	6.80	5.89	5.22	6.95	5.72	7.05	5.85	5.56	5.56
Tree diameter (cm)	31	34	28	28	27	23	39	36 ^f	32	35	31	31

According to Changsheng et al. (1998), the main characteristics of spruce crowns can be estimated from standard tree measurements, such as age, height, and diameter at breast height (DBH). Increasing stand density reduces crown length (Hasenauer and Monserud 1996). Ewald (2005) showed the importance of soil chemistry and stand age in controlling the spruce crown condition, and the close relationship of transparency with other vitality parameters, such as height growth and needle size.

At the same time, a worsening of stand site conditions necessary for *Ips typographus* survival in intensively managed areas, resembling habitat fragmentation, could force more individuals to fly longer distances to find more suitable forested areas in which to settle. Hence, unmanaged protected areas likely offer better ecological conditions to host large beetle populations, reducing the

need for individuals to emigrate long distances to find suitable hosts (Valeria et al. 2016).

Martikainen et al. (1999) also stated that removal of recently dead and weakened trees kept the amount of suitable breeding material low for some species and thus limited the numbers of bark beetles. Schwenke (1996) reported that recently dead trees were not attractive for most primary bark beetles such as *Ips typographus* and so it was much more effective to remove logging residues and trees damaged by abiotic events (storm, snow breakage, etc.). These kinds of management are suggested to decrease the risk of outbreaks, especially in situations where trees are temporarily weakened for some reason and thus pre-disposed to beetle attack (Schwenke 1996). The fast removal of bark beetle-infested host material may also be effective in controlling the internal population.

In the present study, the results also showed that site factors, especially slope aspects (NSA and SSA) and slope positions (USP and LSP) were essential factors for the initiation of spruce bark beetle-caused tree mortality. Notably, in the unmanaged site (HVNP), there was a higher probability of initiation in stands growing on the upper slope position. The statistical results indicated that the main effects and interactions of slope aspect and slope position on stand age, height, bark thickness, basal area, density and tree diameter were all significant (P < 0.001) (Table 4). All stand characteristics showed higher values at the upper slope aspect than at the lower slope position with the exception of mean stand height which had higher values at the lower slope position than at the upper slope position. In general, mean stand age, bark thickness, basal area, stand density and tree diameter were ranked in order as the highly attacked plots > the moderately attacked plots > the slightly attacked plots. On the contrary, mean stand height was ranked in the opposite order as the slightly attacked plots > the moderately attacked plots > the highly attacked plots (Table 2).

Microclimatic and soil conditions modified by site related features such as slope aspects and slope positions could be responsible for those variations in spruce mortality caused by bark beetles (*Ips typographus*). It is generally expected that the poor unhealthy conditions due to the frequent climatic anomalies, elevation, soil characteristics and forest composition can trigger insect infestations (Overbeck and Schmidt, 2012).

Several studies identified southward facing slopes, exposed hilltops, and crests as variables that enhanced infestation risk (Jakuš et al. 2011b, Netherer and Nopp-Mayr 2005, Kautz et al. 2013). Various studies also pointed to a higher infestation risk when the soil water supply was low, and the temperature was high on these terrain features (Dutilleul et al. 2000, Seidl et al. 2007). The results in the present study are also in agreement with the findings of other studies that exposition of *Picea orientalis* stands is a significant factor in the attack risk by *Ips typographus*. It was noted in the present study that the upper slope position received higher levels of stand mortality than the lower slope position. This situation

could be firstly related to increasing of the development and reproduction of *Ips typographus* due to the differences in microclimatic conditions created by topographical landforms, as stated by other authors (e.g. Grodzki et al. 2006). Secondly, it could be related to differences in site quality (soil properties, temperature, moisture etc.) between spruce stands

The effects of temperature on Ips typographus's development and reproduction were investigated by some studies (Christiansen and Bakke 1988, Dolezal and Sehnal 2007). With nonlinear models an optimum temperature of 30 °C for the juvenile development and 28.9 °C for reproduction were calculated by Wermelinger and Seifert (1999). The lower limit of swarming activity and dispersion of Ips typographus is 16.5 °C (Wermelinger 2004). Optimum bark temperature for oviposition and the development of the larvae lies between 29 and 30 °C with the minimum at 11.4 °C (Wermelinger 2004). That is why warm south-facing stands and stand perimeters are preferred by swarming Ips typographus in spring (Overbeck and Schmidt 2012). The number of generations per year is dependent upon temperature. In the northern part of its range, it has one generation a year, but it can complete two generations per year further south (Lauscha et al. 2011). The south-facing aspects receive the greatest amount of solar radiation, hot, dry, and also subjected to rapid changes in seasonal and daily microclimate. In contrast, the north-facing aspects receive the least amount of insolation, cool, moist, and subjected to slow changes in seasonal and daily microclimate. Ridge tops or upper convex slope surfaces are also exposed to intense solar radiation, and experience high wind speeds. Therefore, they are drier than average for the region. At the other extreme, lower slopes with the concave surfaces are sheltered from strong winds, subjected to accumulation of organic matter, and moister than average for the region. The present study was not intended to investigate the effects of temperature on the development, reproduction and numbers of Ips typographus, but the result of a study carried out by Akkuzu et al. (2009) in HVNP, supports the findings of other researchers which showed that higher numbers of Ips typographus were caught by pheromone traps on the south aspect and upper parts of the studied sites than on the north and lower parts.

Table 4. Results of two way ANOVA from the unmanaged site

	Sources	SS	df	MS	F	Eta squared
Mortality	Slope aspect (Sa)	2650.231	1	2650.231	3.381	.031
	Slope position (Sp)	6800.454	1	6800.454	8.675**	.077
	Sa X Sp	24.083	1	24.083	.031	.000
	Error	81526.148	104	783.905		
Age (yr)	Sa	5208.333	1	5208.333	24.903***	.193
	Sp	3490.704	1	3490.704	16.690***	.138
	Sa X Sp	867.000	1	867.000	4.145*	.038
	Error	21751.481	104	209.149		
	Sa	546.750	1	546.750	47.193***	.312
11-1-1-1-1-1-1	Sp	872.676	1	872.676	75.325***	.420
Height (m)	Sa X Sp	.231	1	.231	.020	.000
	Error	1204.889	104	11.585		
	Sa	4.138	1	4.138	18.608***	.152
Parkthickness (cm)	Sp	14.026	1	14.026	63.071***	.378
Barkthickness (cm)	Sa X Sp	.433	1	.433	1.948	.018
	Error	23.127	104	.222		
	Sa	8802.083	1	8802.083	48.519***	.318
Basal area	Sp	20972.454	1	20972.454	115.606***	.526
(m²ha-1)	Sa X Sp	2670.083	1	2670.083	14.718***	.124
	Error	18867.037	104	181.414		
	Sa	106.664	1	106.664	23.829***	.186
	Sp	289.919	1	289.919	64.768***	.384
Stand density	Sa X Sp	3.166	1	3.166	.707	.007
	Error	465.533	104	4.476		
	Sa	1358.231	1	1358.231	30.311***	.226
	Sp	8233.787	1	8233.787	183.752***	.639
Tree diameter (cm)	Sa X Sp	154.083	1	154.083	3.439	.032
	Error	4660.148	104	44.809		

Asterisks refers the level of significance: *P<0.05; **P<0.01; ***P<0.001. SS: Sum-of-squares, df: degrees of freedom, MS: Mean squares.

The effects of temperature on Ips typographus's development and reproduction were investigated by some studies (Christiansen and Bakke 1988, Dolezal and Sehnal 2007). With nonlinear models an optimum temperature of 30 °C for the juvenile development and 28.9 °C for reproduction were calculated by Wermelinger and Seifert (1999). The lower limit of swarming activity and dispersion of *Ips typographus* is 16.5 °C (Wermelinger 2004). Optimum bark temperature for oviposition and the development of the larvae lies between 29 and 30 °C with the minimum at 11.4 °C (Wermelinger 2004). That is why warm south-facing stands and stand perimeters are preferred by swarming Ips typographus in spring (Overbeck and Schmidt 2012). The number of generations per year is dependent upon temperature. In the northern part of its range, it has one generation a year, but it can complete two generations per year further south (Lauscha et al. 2011). The south-facing aspects receive the greatest amount of solar radiation, hot, dry, and also subjected to rapid changes in seasonal and daily microclimate. In contrast, the north-facing aspects receive the least amount of insolation, cool, moist, and subjected to slow changes in seasonal and daily microclimate. Ridge tops or upper convex slope surfaces are also exposed to intense solar radiation, and experience high wind speeds. Therefore, they are drier than average for the region. At the other extreme, lower slopes with the concave surfaces are sheltered from strong winds, subjected to accumulation of organic matter, and moister than average for the region. The present study was not intended to investigate the effects of temperature on the development, reproduction and numbers of *Ips typographus*, but the result of a study carried out by Akkuzu et al. (2009) in HVNP, supports the findings of other researchers which showed that higher numbers of *Ips typographus* were caught by pheromone traps on the south aspect and upper parts of the studied sites than on the north and lower parts.

Among the stand characteristics in the present study, the stand age was positively correlated to the percent

mortality rates (r=0.916) in the HVNP site (Table 5). The stand density (r=0.814) was the second-best factor correlating with the percent mortality. The bark thickness which was reported by Grünwald (1986) as a key or limiting factor for bark beetle attacks was the third-best factor with the percent mortality rates in the unmanaged site.

Table 5. Spearman correlation coefficients (r) between mortality and stand characteristics for the unmanaged site (the HVNP)

Mortality	A = 0	Hoight	Bark	Dacal area	Stand	Tree
Mortality	Age	пеідпі	thickness	Basai area	density	diameter
-						
0.916***	-					
-0.445**	-0.305**	-				
0.768**	0.833**	-0.479**	-			
0.731**	0.769**	-0.401**	0.817**	-		
0.814**	0.823**	-0.450**	0.853**	0.940**	-	
0.594**	0.628**	-0.491**	0.812**	0.840**	0.837**	-
	0.916*** -0.445** 0.768** 0.731** 0.814**	0.916*** -0.445** -0.768** 0.731** 0.769** 0.814** 0.823**	0.916*** -0.445** -0.768** 0.731** 0.769** -0.401** 0.814** 0.823** -0.450**	Mortality Age Height thickness	Mortality Age Height thickness Basal area	Mortality Age Height thickness Basal area density

^{*}Correlation is significant at the 0.05 level (two-tailed).

The stand age and exposition of spruce stands were mostly reported to be related to their susceptibility to bark beetle attack (Overbeck and Schmidt 2012, Mezei et al. 2014). The preference of Ips typographus to attack older trees with a larger diameter was shown by some researchers (e.g. Becker and Schröter 2001, Seidl et al. 2007). According to Becker and Schröter (2001), trees over 70 years old were prone to bark beetle attacks, and Netherer and Nopp-Mayr (2005) found that trees over 100 years old were the most susceptible. Similar to these findings, oriental spruce trees that were less than 100 years old from the Saçınka site (average age 83 years old) (Table 3) were less prone to bark beetle attacks compared to spruce trees over 100 years old from the Hatila Valley National Park (average age 113 years old) (Table 2). Larger diameter trees can provide a more suitable habitat or food source for attacking adults and developing offspring because of increased phloem thickness (Bleiker et al. 2003). Many authors have reported (Dymerski et al., 2001, Jenkins et al., 2014) reported that larger diameter Engelmann spruce trees (Picea engelmanni Parry) were preferenced by different spruce beetle (Dendroctonus rufipennis Kirby).

As observed by Larsson et al. (1983) for ponderosa pine, the results of the present study indicated that Picea orientalis vigor decreased as stand density increased. Dead trees were usually located in an area with older trees and higher stand density, especially on the south aspect and the upper slope position. The importance of stand age and density found in the present study are in agreement with the results of Hilszczanski et al. (2007) in boreal forests. Ozaki et al. (1998) obtained similar results in the case of an Ips typographus attack on Picea jezoensis. They confirmed the positive relationship between the proportion of dead stems and stem density of spruce. The fact that Picea orientalis stands become less dense with increasing age and thus become partially warmer, may be favorable to the beetles' development (Overbeck and Schmidt 2012). Some researchers and foresters emphasized that the amount of bark-beetlecaused tree mortality in spruce forests could be decreased by reducing tree competition and increasing individual tree growth by thinning, while others pointed out using shorter rotation times, and maintaining multiple tree species and age classes (Fettig et al. 2007).

^{**}Correlation is significant at the 0.01 level (two-tailed).

The effects of aspect and slope position on species composition, development, productivity, environmental conditions and soil characteristics were well investigated (Sariyildiz et al., 2005). The comparative trend of pH on north versus south aspects in the present study (lower on north slopes) is similar to the pattern observed by Kutiel (1991), but the reverse of pH trends in studies in the humid eastern United States: Franzmeier et al. (1968) in the Cumberland Plateau. Losche et al. (1970) in the southern Appalachians, Hutchins et al. (1976) in Kentucky, and Boemer (1984) in southern Ohio. Boerner (1984) reported that, despite similar parent materials, soils of north-facing sites had higher pH, soil organic matter, extractable nitrogen concentrations, and base saturation than those of south-facing sites. In a southern Appalachian watershed, Losche et al. (1970) found that soil pH and nutrient availability were highest on northfacing site, intermediate on south-facing sites, and lowest on ridge tops. They stated that kaolin and the pedogenic 2:1–2:2 intergrade minerals were predominant in the soils of the north-facing landscapes, whereas, gibbsite was the major clay mineral in the soils of the south-facing landscape. Low nutrients and low moisture levels or other abiotic stresses may increase the concentrations of sugar and other usable substances in foliage or create a more favorable balance of nutrients (Mopper and Whitham 1992). Mopper et al. (1990) showed that pinyon pines growing on less severe (lower mean temperatures, higher soil moisture, higher nutrient availability, and finer particle sizes) sandy loam soils adjacent to cinder fields were rarely attacked and exhibited normal reproduction and growth. They stated that trees on sandy-loam soil produced the least amount of resin and yet exhibited the lowest levels of herbivory. Thus, when the incidence of herbivory was low, the defense was not as critical, and photosynthate was used primarily for growth rather than for defense.

In addition to all those sites favoring factors due to forest management activities, the results in the present study have also shown that forest management activities can significantly improve soil properties on *Picea orientalis* stands and may decrease the likelihood of *Ips typographus* attacks on individual trees and stands in the managed site (the SFSD). In the present study, mean soil

pH, OM, nutrients, percent clay and silt content were lower (except sand and C to N ratio) in HVNP sites than in SFSD sites (Table 6).

In general, SFSD had higher N, Ca and Mg levels, but lower P and K levels than HVNP (Table 6). At both sites, all soil macronutrients (N, P, K, Ca and Mg) were higher at the lower slope position than at the upper slope position (Table 6). Soil macronutrients (N, P, Ca and Mg) were mostly higher on NSA than on SSA. SFSD showed higher Cu, Zn and Fe levels, but lower Mn and Na levels than those on HVNP (Table 6). At HVNP, mean Mn, Zn and Fe levels were higher on NSA than on SSA, while mean Cu level was higher on SSA.

Forest health is strongly dependent on soil conditions and the adaptation of plants to given states of soil structure, acidity or nutrient availability (Jactel et al. 2009). Soil nutrients and soil pH were previously shown to influence spruce bark beetle attacks on trees (Dutilleul et al. 2000). This may be an indication of leaching soil nutrients from the topsoil through the subsoil in HVNP site due to the lower canopy closure after the insect-damaged in the stands.

In conclusion, this study has indicated that stand characteristics and soil properties of Picea orientalis which vary significantly with forest management activities can have a significant effect on the intensity of I. typographus attack. Topography (slope aspects and slope positions) seems to be a more critical factor in the intensity of I. typographus attack for the unmanaged sites than the managed site. Picea orientalis stands with high variables (especially older trees, high stand density and bark thickness) can be more susceptible to I. typographus attack compared to the stands with low variables, while the stands with low soil quality (especially low nutrients and organic matter) can enhance I. typographus attack. To prevent I. typographus outbreak the first aim should be to maintain healthy trees and stands by forest management practices such as thinning, pruning and cleaning. These practices may also minimize the probability of environmental stress and reduce any bark beetle attacks

Table 6. Mean values for some soil properties according to management, slope position and slope aspects

		N	SA		SSA					
	Unmana	Unmanaged site		Managed site		aged site	Managed site			
	USP	LSP	USP	LSP	USP	LSP	USP	LSP		
pН	4.62±0.24	4.86±0.25	4.85±0.33	4.91±0.41	4.74±0.21	4.06±0.42	5.29e±0.27	5.00e±0.43		
OM (%)	3.64±0.64	4.00±0.32	4.51±0.22	5.96±0.17	4.39±0.42	4.88±0.11	5.59 ^d ±0.09	4.67°±0.13		
Sand (%)	90±2	66±2	71±2	57±3	68±2	69±3	69 ^b ±3	66±2		
Clay (%)	2±1	21±2	16±2	23±1	14±2	16±1	16 ^b ±2	18 ^d ±2		
Silt (%)	7±0	13±1	14±0	20±2	18±2	15±1	15b±1	15±1		
N (%)	0.21±0.02	0.30±0.02	0.36±0.04	0.49±0.05	0.20±0.02	0.28±0.03	0.45±0.05	0.43±0.04		
P (mg/kg)	8.99±1.65	8.73±1.40	8.86±1.52	8.98±1.64	6.84±0.84	8.83±1.50	6.24±1.24	8.19±0.86		
K (mg/kg)	99±8	101.3±7	72.0±4.33	82.3±6.67	81.3±8	118.7±10.3	67.00±6	95.3±7		
Ca (mg/kg)	291.3±24.7	533.3±24	708.7±15	1687.3±29	386.3±27	307.0±28.7	758.00±24.3	1479.3±25		
Mg (mg/kg)	52.9±7.67	138.7±9	104.0±8.67	269.3±12.7	71.2±6	72.3±5	147.00±5.33	359.0±13		
Mn (mg/kg)	22.3±4.33	46.7±4	22.1±3	23.6±2.67	18.7±3	16.3±2.33	8.86±1.67	24.4±3		
Cu (mg/kg)	0.35±0.03	0.65±0.07	0.87±0.09	1.16±0.16	0.62±0.06	0.61±0.05	0.60±0.06	1.11±0.05		
Zn (mg/kg)	1.50±0.27	1.28±0.12	4.26±0.60	1.64±0.28	0.77±0.19	1.34±0.09	1.65±0.07	2.02±0.19		
Fe (mg/kg)	131.0±20.3	137.0±13.7	227.7±22.3	124.0±12.3	94.3±9	138.0±13	137.0±14	131.0±14		
Na (mg/kg)	17.33±3	14.1±1.77	13.8±1.5	12.6±2.24	17.2±1.53	14.3±1.33	8.81±0.78	16.7±0.39		

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REFERENCES

- Akkuzu E, Sariyildiz T, Kucuk M, Duman A (2009) *Ips typographus* (L.) and *Thanasimus formicarius* (L.) populations influenced by aspect and slope position in Artvin-Hatila valley national park, Turkey. Afr J Biotechnol 8(5):877–882
- Allen SE (1989) Chemical Analysis of Ecological Materials. Blackwell Scientific Publications, Oxford.
- Becker T, Schröter H (2001) Die ausbreitung des borkenkäferbefalls im bereich von sturmwurf-sukzessionsflächen. Berichte Freiburger Forstliche Forschung, Baden– Württemberg.
- Bleiker KP, Lindgren BS, Maclauchlan LE (2003) Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleopteran: Scolytidae). Can J For Res 33:1538-1543
- Boerner RE (1984) Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio. Can J For Res 14:794-802
- Can A (2018). Quantitative data analysis by scientific research process with SPSS (SPSS ile bilimsel Araştırma sürecince nicel very analizi). 6th eds. PEGEM Akademi, Ankara
- Changsheng L, Jianfeng S, Yongfang X, Colin F, Houllier F (1998) Crown morphology of Norway spruce from usual tree measurements. J For Res 9(1):8-12
- Christiansen E, Bakke A (1988) The spruce bark beetle of Eurasia. In: Dynamics of Forest Insect Populations. Ed. by Berryman, A.A., Plenum Publishing Corporation, New York, 479-503.
- Dolezal P, Sehnal F (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. J Appl Entomol 131:165-173
- Dutilleul P, Nef L, Frigon D (2000) Assessment of site characteristics as predictors of the vulnerability of Norway spruce (*Picea abies*

- Karst.) stands to attack by *Ips typographus* L. (Col., Scolytidae). J Appl Entomo 124:1-5
- Dymerski AD, Anhold JA, Munson AS (2001) Spruce beetle (*Dendroctonus rufipennis*) outbreak in Engelmann spruce (*Picea engelmannii*) in central Utah, 1986-1998. West N Am Nat 61:19-24
- Ewald J (2005) Ecological background of crown condition, growth and nutritional status of Picea abies (L.) Karst in the Bavarian Alps. European J For Res 124:9–18
- Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negron JF, Nowak JT (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For Ecol Manage 238:24-53
- Franzmeier DP, Pederson EJ, Longwell TL, Byme JG, Losche CK (1969) Properties of some soils in the Cumberland Plateau as related to slope aspect and position. Soil Soc Am Proc 33:755-761
- Grünwald M (1986) Ecological segregation of bark beetles (Coleoptera, Scolytidae) of spruce. J Appl Entomol 101:176–187
- Gülçur F (1974) Physical and chemical analyzing methods of soil properties. I.U. For. Faculty. Issue No: 201, İstanbul, Turkey.
- Grodzki W, Loch J, Armatys P (2006) Occurrence of *Ips typographus* (L.) in wind-damaged Norway spruce stands of Kudłoń massif in the Gorce National Park. Ochrona Beskidów Zachodnich, (in Polish, English summary), 1:125-137
- Hasenauer H, Monserud RA (1996) A crown ratio model for Austrian forests. For Ecol Manage 84:49-60
- Hilszczanski J, Gibb H, Bystrowski C (2007) Insect natural enemies of Ips typographus (L.) (Coleoptera, Scolytinae) in managed and unmanaged stands of mixed lowland forest in Poland. J Pest Sci 80:99–107
- Hutchins RB, Blevins RL, Hill JD, White EB (1976) Influence of soils and microclimate on vegetation of forested slopes in eastern Kentucky. Soil Sci 12l:234-241
- Jactel H, Nicoll B.C, Branco M, Gonzales-Olabarria JR, Grodzki W, Långström B, Moreira F, Netherer S, Orazio C, Piou D, Santos H, Schelhaas MJ, Tojic K, Vodde F (2009) The influences of forest stand management on biotic and abiotic risks of damage. Annals of Forest Science, Springer Verlag/EDP Sciences, 66 (7), 4.

- Jactel H, Branco M, Duncker P, Gardiner B, Grodzki W, Langstrom B, Moreira F, Netherer S, Nicoll B, Orazi C, Piou D, Schelhaas MJ, Tojic K (2012) A Multicriteria Risk Analysis to Evaluate Impacts of Forest Management Alternatives on Forest Health in Eur Ecol Society 17(4), 52.
- Jakuš R., Edwards-Jonášová M, Cudlín P, Blaženec M, Ježík M, Havlíček F, Moravec I (2011a) Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. Trees 25:965–973
- Jakuš R, Zajíčkova L, Cudlín P, Blaženec M, Turčani M, Ježík M, Lieutier F, Schlyter F (2011b) Landscape-scale *Ips typographus* attack dynamics: From monitoring plots to GIS-based disturbance models. iForest 4:256–261
- Jenkins MJ, Hebertson EG, Munson AS (2014) Spruce Beetle Biology, Ecology and Management in the Rocky Mountains: An Addendum to Spruce Beetle in the Rockies. Forests 5(1):21-71
- Kalra YP, Maynard DG (1991) Methods Manual for Forest Soil and Plant Analysis. Forestry Canada, Northern Forestry Publications. Alberta, Canada.
- Kautz M, Schopf R, Ohser J (2013) The "sun-effect": microclimatic alterations predispose forest edges to bark beetle infestations. Eur J For Res 132:453–465
- Keskinalemdar E, Alkan Ş, Aksu Y (1987). Artvin ilinde *Ips typographus* L. (Coleoptera:Scolytidae)'in Biyolojisi ve mücadelesi üzerine çalışmalar. Türkiye 1'inci Entomolojisi kogresi bildirileri, İzmir, 737-742.
- Kutiel P (1992). Slope aspectt effect on soil and vegetation in a Mediterranean ecosystem. Israel Journal of Botany, 41, 243-250.
- Larsson S, Oren R, Waring RH, Barrett JW (1983) Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. For Sci 29:395-402
- Lauscha A, Fahse L, Heurich M (2011) Factors affecting the spatiotemporal dispersion of *Ips typographus* (L.) in Bavarian Forest National Park: A long-term quantitative landscape-level analysis. For Ecol Manage 261:233-245
- Losche EK, McCracken RJ, Davey CB (1970) Soils of steeply sloping landscapes in southern Appalachian Mountains. Soil Sci Soc Am 34:473-478.
- Martikainen P, Siitonen J, Kaila L, Punttila P, Rauh J (1999) Bark beetles (coleoptera, Scolytidae) and associated beetle species in mature managed and old growth boreal forests in southern Finland. For Ecol Manage 116:233-245
- Mezei P, Grodzki W, Blaženecac M, Škvareninad J, Brandýsovád V, Jakušac R (2014) Host and site factors affecting tree mortality caused by the spruce bark beetle (*Ips typographus*) in mountainous conditions. For Ecol Manage 331:196–207
- Mopper S, Whitham TG, Price PW (1990) Plant phenotype and interspecific competition between insects determine sawfly performance and density. Ecology 71:2135-2144.
- Mopper S, Whitham TG (1992) The plant stress paradox: effects on pinyon sawfly sex ratios and fecundity. Ecology 73:515-525
- Netherer S, Nopp-Mayr U (2005) Predisposition assessment systems (PAS) as supportive tools in forest management rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. For Ecol Manage 207:99–107

- OGM (2015) General Directorate of Forestry, Turkish Forest, Ankara. https://www.ogm.gov.tr/SitePages/OGM/OGMDefault.aspx
- Overbeck M, Schmidt M (2012) Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). For. Ecol. Manage. 266, 115–125.
- Ozaki K, Fukuyama K, Maet K, Itoh K (1998) Density effects on the conifer mortality in declining spruce-fir forest in northern Japan: implication of bark beetle attack to, cause spruce decline. J For Res 3:231–235.
- Peltonen M, HelioÈvaara K, VaÈisaÈnen R (1997) Forest insects and environmental variation in stand edges. Silva Fennica 31:129-141
- Sariyildiz T, Anderson JM, Kucuk M (2005) Effects of tree species and topography on soil chemistry, litter quality and decomposition in Northeast Turkey. Soil Biol Biochem 37:1695-1706
- Sariyildiz T, Akkuzu E, Küçük M, Duman A, Aksu Y (2008) Effects of *Ips typographus* (L.) damage on litter quality and decomposition rates of Oriental Spruce (*Picea Orientalis* (L.) Link.) in Hatila Valley National Park, Turkey. Eur J For Res 127:429-440.
- Schowalter TD, Filip GM (1993) Beetle-Pathogen Interactions in Conifer Forests. Academic Press, London.
- Schwenke W (1996) Grundzuège des Massenwechsels und der Bekaèmpfung des Groûen Fichtenborkenkaèfers, Ips typographus (L.) (Col. Scolytidae). Anz. Schaèdlingskde., Pflanzenschutz. Umweltschutz 69:11-15
- Seidl R, Baier P, Rammer W, Schopf A, Lexer MJ (2007) Simulating tree mortality from bark beetle infestation in Norway spruce forests. Ecol. Model. 206, 383–399.
- Smith DM (1986) The practice of silviculture, 8th ed., Wiley, New York, NY
- Sohn JA, Gebhardt T, Ammer C, Bauhus J, Häberle KH, Matyssek R, Grams TEE (2013) Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*). For Ecol Manage 308:188-197
- Sproull GJ, Adamus M, Bukowski M, Krzyżanowski T, Szewczyk J, Statwick J, Szwagrzyk J (2015) Tree and stand-level patterns and predictors of Norway spruce mortality caused by bark beetle infestation in the Tatra Mountains. For Ecol Manage 354:261–271
- Väisänen R, Bistroèm O, Helioèvaara K (1993) Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? Biodiversity Conserv 2:95-113
- Valeria M, Coralie B, Petr D, Susanne K, Jan O, Christian S, Yoshan M (2016) How differential management strategies affect *lps typographus* L. dispersal. For Ecol Manage 360:195–204
- Wallin KF, Raffa KF (2004) Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. Ecol Monographs 74:101-116
- Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus*- a review of recent research. For Ecol Manage 202:67-82
- Wermelinger B, Seifert M (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. Ecol Entomol 24:103-110
- Zausen GL, Kolb TE, Bailey JD, Wagner MR (2005) Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. For Ecol Manage 218:291–305