European Journal of Environmental Sciences

CONTENTS

ECOLOGICAL PERSPECTIVE OF THE DIVERSITY OF FUNCTIONAL RESPONSES

AHMAD PERVEZ[1,*], PREET PAL SINGH[2], and HAKAN BOZDOĞAN[3]

[1] Biocontrol Laboratory, Department of Zoology, Radhey Hari Government P. G. College, Kashipur – 244713, Udham Singh Nagar, Uttarakhand, India
[2] Department of Mathematics, Government P. G. College, Rishikesh, Uttarakhand, India
[3] Ahi Evran University, Vocation School of Technical Sciences, Department of Plant and Animal Production, 40100, Kırşehir, Turkey
* Corresponding Author: ahmadpervez@yahoo.com

ABSTRACT

Prey-predator interactions have been modelled by numerous workers. Ecologists have continuously modified Lotka–Volterra equations in order to provide more realistic descriptions of the complexity of these interactions. The response of predator(s) to increasing prey density can be best described in terms of a functional response, which is an important criterion determining the success or failure of predator(s) to control fluctuating prey populations. The functional response of a predator is further differentiated into Holling's Type I, II, III, IV and V. We discuss one-prey and one-predator interactions, in which the models are modified by the inclusion of steady-state satiation and growth factors. We review situations where two prey and one predator interact, and *vice versa*. We also discuss Holling's Type IV model relevant to competition and food chains. There is a need to examine functional responses as these models were mostly developed by pure mathematicians and their relevance to field conditions remains largely untested. Prey-predator interactions can be affected even by small factors and ecologists should include these models in their experimental design when attempting to predict realistic interactions.

Keywords: dynamics; ecology; Holling; modelling; predator; prey

Introduction

Prey-predator interactions stimulated theoretical ecologists to develop equations that described realistic interactions. Lotka (1925) and Volterra (1926) use differential equations to describe these interactions. However, the complexity of prey-predator interactions resulted in subtle modifications in the proposed equations. Nicolson and Bailey (1935) introduced the term "area of discovery" as a variable associated with the attack rate of the predator, which triggered a chain of alterations in Lotka–Volterra models, especially when prey and predator densities are varying. The functional response of a predator describes its rate of prey consumption at different prey densities (Holling 1959, 1965), which can be classified into five types (Type I, II, III, IV and V). Equation $c(x) = mx$ describes the Type I response, in which there is a linear increase in predation rate with prey density up to a threshold (Leslie and Gower 1960; Hsu and Huang 1995). Holling (1959) used Michaelis–Menten's formula (expressed by $c(x) = m / (A + x)$) to describe the Type II functional response in which there is a decelerating increase in predation rate with prey density until satiation is attained (Aziz-Aloui and Okiye 2003; Huu Du et al. 2007).

Holling's Type III response exhibits a sigmoidal increase in predation rate at high prey densities and is described by the equation $c(x) = mx^n / (A + x^n)$. The general form of this type of functional response was developed by Kazarinov and van den Driessche (1978). Type IV response is relatively less studied and describes the condition where the predator per capita predation rate decreases at exceptionally high prey densities, which is expressed by the equation $c(x) = mx^2 / (A + x)(B + x)$ (Tanner 1975; Ali et al. 2016a,b). Type V response, also known as Ivlev's functional response, is described by the equation, $c(x) = m (1 − e^{−Ax})$. Holling's Type II and III responses could also be considered as classical Hill functions (Gesztelyi et al. 2012). However, random perturbations in population dynamics can lead to very different models, which are more realistic simulations (Xianning and Lansun 2003; Bing et al. 2004). This diversity and complexity in prey-predator interactions stimulated us to present here an overview of the mathematical models that may better predict such interactions.

Various types of prey-predator systems

Prey-predator models depend on the nature and quantity of prey and predators. Numerous factors affect predators and their prey. We review a few situations where the predator is expected to behave differently and this change in behaviour possibly affects its functional response.

1. One Prey – One Predator System

There are many functional response studies of one prey and one predator (particularly ladybirds, see book: Hodek et al. 2012). Holling's (1959, 1965) equations did not include the effect of satiation. However, if needed, it might be included in a steady state satiation (SSS) equation (Jeschke et al. 2002) with a constant satiation rate. Jeschke et al. (2002) suggest that digestion should not be incorporated as part of prey handling time (Pervez and Omkar 2003), as it does not prevent foraging. Instead, Jeschke et al. (2002) incorporate hunger level and time lost in unsuccessful attempts to catch prey in their model and named it as steady-state satiation (SSS) equation. In this equation, attack rate (a) is the product of encounter rate

(**β**) between a foraging predator and prey, the probability that the consumer detects encountered food (**γ**), the probability that the consumer attacks detected food (**δ**), and attack efficiency (**ξ**), *i.e.* the frequency of successful attacks (*i.e. a* = **βγδξ**). Handling time (*b*) is the ratio of attack time t_{att} (per food item) and attack efficiency (**ξ**), added to eating time t_{eat} (per food item), i.e. $b = t_{att} / $ **ξ** $+ t_{eat}$. This SSS equation is:

$$y(x) = \begin{cases} \dfrac{1 + ax(b+c) - \sqrt{1 + ax(2(b+c) + ax(b-c)^2)}}{2abcx} & a,b,c,x > 0 \\ \dfrac{ax}{1+abx} & b > 0, c = 0 \\ \dfrac{ax}{1+acx} & b = 0, c > 0 \\ ax & b = c = 0 \\ 0 & a = 0 \text{ or } x = 0 \end{cases}$$

Jeschke and Hohberg (2008) also propose a satiation model that accounts for prey depletion and increasing predator satiation over time.

$$\frac{dy(t)}{dt} = \frac{h(t)ax(t)}{1 + h(t)abx(t)}$$

$$x(t) = x(0) - y(t)$$

Here, the first equation reveals that prey consumption rate increases as a function of hunger level (*h*), attack rate (*a*), prey abundance (*x*) and handling time (*b*).

Liu and Lin (2010) introduce a cross-diffusion parameter in the prey-predator models. They are of the opinion that prey might be able to protect themselves from attacks by predators and hence a resistance parameter should also be incorporated in the model. Recent research also focuses on including the dynamic properties of random perturbations in classical prey-predator models (Liu et al. 2004; Liu and Tan 2007). Randomly perturbed predator-prey models, thereby, have been used by many researchers to describe the efficiency of integrated pest management strategies (Jeschke et al. 2002; Mailleret and Grognard 2009). For managing pest populations specific prey-predator combinations along with pesticide sprays can also work. These models may further be modified by manipulating the predator's stage structure (Georgescu and Zhang 2010), state-dependent random perturbations, age and defence mechanisms of the pests (Zhang and Georgescu 2010), and patch structure of the pests (Yang and Tang 2009). Thus, it is possible to improve the classical models designed for one-prey and one-predator system.

Incorporation of a Growth Factor in the equation

Both prey and predator grow logistically in the field and in certain artificial experimental arenas, as the predator has other food sources besides prey. Thus, the predator has two growth rates, *viz.* predation and logistic growth. Rayungsari et al. (2014) introduce a model that has three equilibrium points, *viz.* the prey extinction point (E_1), predator extinction point (E_2) and survival point (E_2). Here, E_2 is unstable, while the other two are locally asymptotically stable under certain conditions. Sharma and Samanta (2014) describe a similar model and considered two situations, *i.e.* normal and hunger. In this model, fractional derivatives of order **α** and **β** (where $0 < $ **α** ≤ 1; $0 < $ **β** ≤ 1) are considered rather than only the first order time derivatives. In addition, they construct approximate solutions using the Homotopy Perturbation Method and Variation Iteration Method. The modified equations for the above two cases are presented below.

Case 1: For the normal situation, i.e. the functional response is equal to the attack capacity per predator; (when cN ≥ aP):

$$D_t^\alpha N(t) = p\left\{ \frac{r}{\lambda}\left[1 - \left[\frac{N(t)}{k}\right]^\lambda \right] N(t) - aP(t) \right\}$$

$$D_t^\beta P(t) = p(b - d)P(t)$$

Case 2: For the hunger situation, the functional response is smaller than the attack capacity, i.e., if more prey were available, the predator would increase its catch (when cN ≤ aP):

$$D_t^\alpha N(t) = p\left\{ \frac{r}{\lambda}\left[1 - \left[\frac{N(t)}{k}\right]^\lambda \right] - c \right\} N(t) \right\}$$

$$D_t^\beta P(t) = p\left[b\frac{c}{a}N(t) - P(t)\left[d + \frac{1}{T}\ln\left(\frac{aP(t)}{cN(t)}\right) \right] \right]$$

With initial conditions

$$N(0) = c_1; P(0) = c_2$$
$$\text{and } 0 < \alpha \leq 1; 0 < \beta \leq 1$$

Here, $N(t)$ and $P(t)$ denote the population density of prey and predator respectively, whereas the other parameters are *r* (intrinsic growth rate of prey population), *k* (carrying capacity of prey population), *a* (attack capacity of predator population), *b* (birth rate of predator), *c* (maximum predation rate), *d* (natural death rate of predator population) and *T* (the typical time of the response to hunger).

2. Two Prey – One Predator System

It is possible to describe the functional response at multiple tritrophic levels, i.e. ecosystems with many species of prey (Georgescu 2011), predators (Pei et al. 2005) and food chains (Baek 2008). Krivan and Eisner's (2006) two-prey and one-predator model predicts that when prey resources grow exponentially, the prey handling times decrease to almost zero and can result in great differences in prey consumption. This could lead to the extinction of weaker prey. In a different two-prey and one-predator model, the prey handling time depends on comparative prey density that enables the predator to stabilize the system (Green 2004). Here, the prey do not compete and predation follows the density gradient of prey. Kesh et al. (2000) propose a two- prey and one-predator species

model in which the predator dietary functions are ratio-dependent. They predict the conditions that result in the permanent stability of the system. Pal and Mahapatra (2014) introduce an imprecise two prey – one predator model by using interval and fuzzy numbers in the modelling of the prey and predator interaction.

In another two-prey and one-predator model, the intrinsic growth rate of the prey varies periodically in order to incorporate seasonal variations in which the environmental conditions follow a predictable pattern (Song and Xiang 2006). In a similar model using a Lyapunov function, the prey consumption of a single predator increases linearly with increase in density of two species of prey (Chaudhuri and Kar 2004). Thus, it is inevitable that as ecological conditions vary, functional responses have to change and other variables and constants must be incorporated in order to predict more realistic outcomes of prey-predator interactions.

3. One-Prey – Two-Predator System

In one-prey and two-predator systems, the two predators can differ in strength. Hsu (1981) proposes one such model and infers that the top predator is more successful if the interference coefficient is small, while the outcome of predation depends on the initial abundances of the two predators if the interference coefficient is large. However, the criterion for persistence and stability in such systems was proposed later by Freedman and Waltman (1984) and Gopalsamy (1986). The fate of the two predators attacking a single prey and their co-existence depends on the ratio between their numerical responses (Mitra et al. 1992). Dubey and Das (2000) propose a model for two predators foraging for a single species of prey based on a Gause-type model. In this, the predators compete with one another when prey are scarce. Dubey and Upadhyay (2004) propose another model for one prey and two predator interactions and discuss the factors resulting in either persistence or extinction. Alebraheem's (2012) model indicates that coexistence of two predators (y and z) depends on the efficiencies of the predators' conversion of prey biomass into predator offspring being similar. However, if they differ the predator with the lower value becomes extinct. Sunaryo et al. (2013) propose a similar model in which both the top and second predator have Type III functional responses. This model predicts two equilibrium points and a switch from instability to stability known as Hopf bifurcation. Garay et al. (2015) suggest that in two-predator systems there will be a higher incidence of fighting and lower incidence of killing prey. Experimental studies reveal that in such scenarios the two predators can work in tandem by complimenting each other. Laboratory experiments indicate a synergistic effect on prey mortality when two ladybird-predators (Coleoptera: Coccinellidae) attack the same population of aphids (Homoptera: Aphididae) (Omkar and Pervez 2004, 2011). The mortality of pea aphids (*Acyrthosiphon pisum)* infesting a crop of alfalfa

(*Medicago sativa*) increases many-fold when attacked by three natural enemies, viz. a ladybird beetle *Harmonia axyridis* (Pallas), damsel bug *Nabis* sp. and parasitic wasp *Aphidius ervi* (Cardinale et al. 2003).

Holling Type IV Model for Describing Competition / Food Chains

Andrews (1968) suggests a function known as the Monod-Haldane function (*i.e.* $p(x) = mx / (a + bx + x^2)$, which is also known as Holling's Type IV function with a non-monotonic equation. It may also be written as: $g(N,P) = aN / (1 + bN + aN^2)$. This equation was further simplified by Sokol and Howell (1987) who assume that $b = 0$, which nullifies the bN part of the denominator.

Shuwen et al. (2005) investigate two-species predator–prey systems using Holling's Type IV response with predator subject to random perturbations. Funasaki and Kot (1993) report chaos in a periodically pulsed mass-action chemostat. Venkatesan et al. (2003) discuss the presence of a multiple period-doubling bifurcation route to chaos in periodically pulsed chaotic dynamic systems. Baek et al. (2009) describe conditions for the stability of a food chain using Holling type IV functional response and the Floquet theory of impulsive equations and small perturbations. Upadhyay et al. (2011) studied a model system subject to environmental driving forces that are unable to drive the system from a regime of deterministic chaos towards a stochastically stable situation. Upadhyay and Raw (2011) study the complex dynamics of a three-species food chain using a Holling Type IV functional response and report chaotic behaviour in a narrow region of the bifurcation parameter space for biologically realistic parameter values. Ali et al. (2016b) infer that increasing or decreasing the top predator's intrinsic growth rate can change the dynamics of food chains from chaotic to asymptotically stable. In addition, an increase in the death rate of the middle predator can stabilize the dynamics of this system.

Some predator-prey systems include two predator species attacking a single species of prey. Of the two predators, the top predator attacks both the prey and the second predator when the prey is scarce. Different approaches simulate the complex interactions of this multi-predator system with prey density or extra guild prey, which are complicated, multi-variant and chaotic (Funasaki and Kot 1993; Venkatesan et al. 2003; Shuwen et al. 2005). In such circumstances or in food chains, complex simultaneous functional responses occur. A depletion in prey density affects the attack rate of the top predator (X) and second predator (Y). Simultaneously, the density of Y will also decrease because of X. Zhang and Chen (2005) present a modified model that may depict the outcome of these complex interactions.

Cosner and de Angelis (1999) introduce the concept of the effect of spatial grouping on the functional response of predators. They state that if predators have a homogenous spatial distribution, then a prey depend-

ent functional response can be expected. However, when shoals of predators hunt for prey, the functional response will be both predator and prey dependent. This results in the predator density having a significant effect on the functional response, which is then dependent on predator density and the encounter rate. Many predators become confused on encountering a swarm of prey, which negatively affects their predation rate (Jeschke and Tollrian 2005). At high prey densities, it may restrict the predator's neuronal abilities, which makes them less successful in attacking prey (Krause and Ruxton 2002). Predator confusion significantly affects the functional response, however, this effect is not included in traditional models (Jeschke and Tollrian 2005). Most of these models only describe the ecological interaction between predator and prey. In predator confusion situations, usually the functional response is dome-shaped, indicating a dramatic dip in the predation rate at high densities. Predator confusion is widespread and occurs in many animal systems. Interestingly, predator-prey theory, especially functional response models, do not include it as a factor reducing predation rate. This is addressed by Jeschke and Tollrian (2005) in their elaborate model based on the SSS equation proposed by Jeschke et al. (2002). Olson et al. (2013) indicate that swarming evolves as an emergent behaviour in prey when a simple perceptual constraint, predator confusion, is imposed on the predator. In addition, measuring swarm density and dispersion serves as a useful alternative for qualitative assessment of every swarm (Huepe and Aldana 2011).

Conclusion

It is evident from this overview that functional responses are highly sensitive to biological and ecological changes. We describe a couple of models in detail just to emphasize the importance of variables that are often neglected by biologists in functional response studies. A subtle change in ecological conditions directly or indirectly affects the possible outcome of prey-predator interactions. Hence, models that incorporate all the major and minor factors that may affect them should be developed. Although there is a plethora of mathematical models, which include many of the factors that affect functional response, they are rarely used or tested by ecologists. Hence, there is an urgent need to test these models using both laboratory and field studies.

Acknowledgements

REFERENCES

Alebraheem J (2012) Persistence of predators in a two predators-one prey model with non-periodic solution. Appl Math Sci 6: 943–956.

Ali SJ, Arifin NM, Naji RK, Ismail F, Bachok N (2016a) Dynamics of Leslie-Gower model with simplified Holling Type IV functional response. J Nonlin Sys Appl 5: 25–33.

Ali SJ, Arifin NM, Naji RK, Ismail F, Bachok N (2016b) Boundedness and Stability of Leslie–Gower Model with Sokol–Howell Functional Response. In: Kiliçman A et al. (eds) Recent Adv Math Sci, pp 13–26.

Andrews JF (1968) A mathematical model for the continuous culture of macroorganisms utilizing inhibitory substrates. Biotech Bioeng 10: 707–723.

Aziz-Aloui MA, Okiye MD (2003) Boundedness and Global Stability for a Predator-Prey Model with Modified Leslie-Gower and Holling-Type II Schemes. Appl Math Letters 16: 1069–1075.

Baek H (2008) Dynamic complexities of a three-species Beddington-DeAngelis system with impulsive control strategy. Acta Applicandae Mathematicae 110: 23–38.

Baek H, Do Y, Saito Y (2009) Analysis of an impulsive predator-prey system with Monod-Haldane functional response and seasonal effects. Math Prob Eng, pp 1–16.

Bing L, Yujina Z, Lansun C (2004) Dynamic complexities of a Holling I predator–prey model concerning biological and chemical control. Chaos, Solitons and Fractals 22: 123–34.

Cardinale BJ, Harvey CT, Gross K, Ives AR (2003) Biodiversity and biocontrol: Emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystems. Ecol Lett 6: 857–865.

Chaudhuri KS, Kar TK (2004). Harvesting in a two prey – one predator fishery: a Bio economic-model. Anziam J 45: 443–456.

Cosner C, de Angelis DL (1999) Effects of Spatial Grouping on the Functional Response of Predators. Theor Pop Biol 56: 65–75.

Dubey B, Das B (2000) Modelling the interaction of two predators competing for a prey in a diffusive system. Ind J Pure Appl Math 31: 823–837.

Dubey B, Upadhyay RK (2004) Persistence and extinction of one-prey and two-predator system. Nonlinear Analysis: Modelling and Control 9: 307–329.

Freedman HI, Waltman P (1984) Persistence in models of three interacting predator prey populations. Math Biosci 68: 213–231.

Funasaki E, Kot M (1993) Invasion and Chaos in a Periodically Pulsed Mass-Action Chemostat. Theor Pop Biol 44: 203–224.

Garay J, Varga Z, Gámez M, Cabello T (2015) Functional response and population dynamics for fighting predator, based on activity distribution. J Theor Biol 368: 74–82.

Georgescu P (2011) On the impulsive control of a n-prey and one-predator food web model: In: Dumitriu NA, Georgescu P, Strugariu R (eds), Proc Int Conf Appl Pure Math, Iasi, Romania, Bull Inst Pol Iasi LVII(LXI): 111–123.

Georgescu P, Zhang H (2010) An impulsively controlled predator-pest model with disease in the pest. Nonlin Anal Real World Appl 11: 270–287.

Gesztelyi R, Zsuga J, Kemeny-Beke A, Varga B, Juhasz B, Tosaki A (2012) The Hill equation and the origin of quantitative pharmacology. Arch Hist Exact Sci 66: 427–438.

Gopalsamy K (1986) Convergence in resource based competition system. Bull Math Biol 48: 681–699.

Green E (2004) The effect of a 'smart' predator in a one predator, two prey system. https://www.rose-hulman.edumathjournal/archives/2004/vol5-n2/paper5/v5n2-5pd.pdf.

Hodek I, van Emden HF, Honek I (2012) Ecology and behavior of the ladybird beetles (Coccinellidae). Wiley-Blackwell, Oxford, UK.

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Ent 91: 385–398.

Holling CS (1965) Functional response of predators to prey density and its role in mimicry and population regulation. Mem Ent Soc Canada 45: 3–60.

Hsu SB (1981) On a resource based ecological competition model with interference. J Math Biol 12: 45–52.

Hsu SB, Huang TW (1995) Global stability for a class of predator-prey systems. Siam J Appl Math 55: 763–783.

Huepe C, Aldana M (2011) New tools for characterizing swarming systems: A comparison of minimal models. Physica A 387: 2809–2822.

Huu Du N, Man NM, Trung TT (2007) Dynamics of predator-prey population with modified Leslie-Gower and Holling-type II schemes. Acta Math Vietnam 32: 99–111.

Jeschke JM, Hohberg K (2008) Predicting and testing functional responses: An example from a tardigrade-nematode system. Basic Appl Ecol 9: 145–151.

Jeschke JM, Tollrian R (2005) Effects of predator confusion on functional responses. Oikos 111: 547–555.

Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. Ecol Monogr 72: 95–112.

Kazarinov N, van den Driessche P (1978) A model predator-prey systems with functional response. Math Biosci 39: 125–134.

Kesh D, Sarkar AK, Roy AB (2000) Persistence of two prey - one predator system with ratio dependent predator influence. Math Meth Appl Sci 23: 347–356.

Krause J, Ruxton GD (2002) Living in Groups. Oxford University Press, Oxford.

Krivan V, Eisner J (2006) The effect of Holling Type II functional response on apparent competition. Theor Pop Biol 70: 421–430.

Leslie PH, Gower JC (1960) The properties of a stochastic model for the predator-prey type of interaction between two species. Biometrika 47: 219–234.

Liu J, Lin Z (2010) Stationary patterns for a predator-prey model with Holling type III response function and cross-diffusion. Bull Korean Math Soc 47: 251–261.

Liu B, Zhi Y, Chen L (2004) The dynamics of a predator-prey model with Ivlev's functional response concerning integrated pest management. Acta Math Appl Sin Engl Ser 20: 133–146.

Liu Z, Tan R (2007) Impulsive harvesting and stocking in a Monod-Haldane functional response predator-prey system. Chaos, Solitons and Fractals 34: 454–464.

Lotka AJ (1925) The Elements of Physical Biology, Williams and Wilkins, Baltimore.

Mailleret L, Grognard F (2009) Global stability and optimisation of a general impulsive biological control model. Math Biosci 221: 91–100.

Mitra D, Mukherjee D, Roy AB (1992) Permanent coexistence in a resource-based competition system. Ecol Model 60: 77–85.

Nicholson AJ, Bailey VA (1935) Balance of animal populations. Part- I. Proc. Soc. London 3: 551–598.

Olson RS, Knoester DK, Adami C (2013) Critical interplay between density-dependent predation and evolution of the selfish herd. Proc Gen Evol Comp Conf (GECCO), pp 1–8.

Omkar, Pervez A (2004) Functional and numerical responses of *Propylea dissecta* (Mulsant) (Col., Coccinellidae). J Appl Ent 128: 140–146.

Omkar, Pervez A (2011) Functional Response of two aphidophagous ladybirds searching in tandem. Biocont Sci Tech 21: 101–111.

Pal D, Mahapatra GS (2014) A bioeconomic modeling of two-prey and one-predator fishery model with optimal harvesting policy through hybridization approach. Appl Math Comp 242: 748–763.

Pei Y, Chen L, Zhang Q, Li C (2005) Extinction and permanence of one-prey multi-predators of Holling type II function response system with impulsive biological control. J Theor Biol 235: 495–503.

Pervez A, Omkar (2003) Predation potential and handling time estimates of a generalist aphidophagous ladybird, *Propylea dissecta*. Biol Memoirs 29: 91–97.

Rayungsari M, Kusumawinahyu WM, Marsudi (2014) Dynamical analysis of predator-prey model with ratio-dependent functional response. Appl Math Sci 8: 1401–1410.

Sharma S, Samanta GP (2014) Dynamical behaviour of a two prey and one predator system. Differ Equa Dyn Syst 22: 2125–145.

Shuwen Z, Lingzhen D, Lansun C (2005) The study of predator–prey with defensive ability of prey and impulsive perturbations on the predator. Chaos, Solitons and Fractals 23: 631–643.

Sokol W, Howell JA (1987) The kinetics of phenol oxidation by washed cells. Biotech Bioeng 30: 921–927.

Song X, Xiang Z (2006) The prey-dependent consumption two – prey one- predator models with stage structure for the predator and impulsive effects. J Theor Biol 242: 683–698.

Sunaryo MSW, Salleh Z, Mamat M (2013) Mathematical model of three species food chain with Holling type-III functional response. Int J Pure Appl Math 89: 647–657.

Tanner JT (1975) The stability and intrinsic growth rate of prey and predator populations. Ecol 56: 855–867.

Upadhyay RK, Raw SN (2011) Complex dynamics of a three species food-chain model with Holling type IV functional response. Nonlinear Analysis: Modelling and Cont 16: 353–374.

Upadhyay RK, Banerjee M, Parshad RD, Raw SN (2011) Deterministic chaos versus stochastic oscillation in a prey-predator-top predator model. Math Model Anal 16: 343–364.

Venkatesan A, Parthasarathy S, Lakshmanan M (2003) Occurrence of multiple period-doubling bifurcation route to chaos in periodically pulsed chaotic dynamical systems. Chaos, Solitons and Fractals18: 891–898.

Volterra V (1926) Variazioni e uttuazioni del numero di individui in specie animali conviventi. Mem Accad Linc 2: 31–113.

Xianning L, Lansun C (2003) Complex dynamics of Holling type II Lokta–Voltrra predator–prey system with impulsive perturbations on the predator. Chaos, Solitons and Fractals 16: 311–320.

Yang J, Tang S (2009) Effects of population dispersal and impulsive control tactics on pest management. Nonlinear Anal Hybrid Syst 3: 487–500.

Zhang S, Chen L (2005) A Holling II functional response food chain model with impulsive perturbations. Chaos, Solitons and Fractals 24: 1269–1278.

FORAGING BEHAVIOUR OF PREDACEOUS LADYBIRD BEETLES: A REVIEW

AHMAD PERVEZ[1],* and MEENA YADAV[2]

[1] Biocontrol Laboratory, Department of Zoology, Radhey Hari Govt. P. G. College, Kashipur, US Nagar – 244713, Uttarakhand, India.
[2] Department of Zoology, Maitreyi College, New Delhi – 110021, India.
* Corresponding author: ahmadpervez@yahoo.com

ABSTRACT

We review the foraging behaviour of predaceous ladybirds in the light of current knowledge. Ladybirds should forage optimally to maximise their resources; however, they are limited – among other things – by their poor visual acuity. Ladybird foraging behaviour includes location of the habitat of its prey, location of prey and prey-selection. Chemical cues are important in locating the habitats of their prey. This is further driven by volatiles or semiochemicals emitted by injured plants, particularly in response to attack by herbivores. Various chemicals induce positive electroantennographic responses in ladybirds that guide them to prey sites. Honeydew secreted by aphids along with alarm pheromones or kairomones act as secondary chemical cues that narrow the search from extensive to intensive and help in prey location. Visual cues further aid prey-location and enable foraging adults to locate areas with patchy or abundant prey. Thereafter, ladybirds select their prey, which starts with random attacks that result in prey selection in terms of size and palatability. Prey selection seems to be host plant driven, i.e. aphids sequester host plant chemicals, which are imbibed by ladybirds. This is evident from the fact that nutritious prey cultured on toxic host plants are usually less preferred or rejected. Foraging ladybirds, especially larvae, can perceive ladybird footprints or odours that deter them from foraging. The above information could be useful in biocontrol programmes in which foraging ladybirds are manipulated by using chemicals as attractants or rearing aphids on nutritious host plants.

Keywords: aphids; Coccinellidae; cues; searching behaviour; semiochemicals

Introduction

Ladybird beetles (Coleoptera: Coccinellidae) are economically important predaceous insects having a wide prey range (Dixon 2000; Omkar and Pervez 2004a; Pervez and Omkar 2004; Hodek et al. 2012; Omkar and Pervez 2016). Their foraging behaviour is well studied because of their biocontrol potential. Riddick (2017) attempted to identify the conditions suitable for the biocontrol of aphids using ladybirds, in terms of their foraging potential in greenhouses. Hodek and Evans (2012) consider the foraging behaviour of ladybirds to be an important aspect of their relationships with food and reproduction. To become successful foragers, these ladybirds might experience a trade-off between the time available for foraging and the availability of prey (Heit et al. 2007). However, ladybirds are reported walking aimlessly in dense aphid colonies, even walking over aphids and leaving them unharmed (Murdie 1971). Hence, ladybirds are also referred to as 'blundering idiots', as pointed out by Hodek and Evans (2012).

Initially, the researches focussed on behavioural aspects of ladybirds related to foraging. This was followed by theories and formulating hypotheses that need empirical testing in terms of the dynamics of foraging patterns in ladybirds. The area concentrated search foraging model (Wiens 1976) states that predators, for example, ladybirds, initially forage extensively for patches of prey and once found switch to searching intensively and consuming prey. However, if prey is absent or rare predators forage more extensively by quickly moving in straight lines and rarely halting (Ferran and Dixon 1993), thereby minimizing the wastage of time and energy. Hodek and

Evans (2012) while reviewing food relationships in ladybirds, commented that progress in the field of chemoecology helped in better understanding the intricacies of coccinellid foraging behaviour. Hence, there is a need to present updated information on foraging behaviour, especially in the light of advances in chemoecology. We review the literature, with an emphasis on current knowledge, to better understand the foraging patterns of coccinellids. We concentrated on the cues used by ladybirds to locate their habitats and in searching and selecting their prey. Issues regarding how their foraging ability can be manipulated are also addressed.

Optimal Foraging and the Prospects of Using Ladybirds in Biocontrol

Foraging ladybirds in search of food and oviposition sites visit many patches of prey (Dixon 2000). Optimal foraging theory assumes that predators decide and select optimal food resources to maximize their rate of food intake and hence improve their fitness and reproduction (Stephen and Krebs 1986). According to the optimal foraging theory, ladybirds should select the most profitable prey and reject unprofitable prey (Crawley and Krebs 1992). However, a few of the assumptions of this model, for instance, predators should estimate the profitability of a patch of prey even before entering it, are unrealistic due to the poor visual acuity of ladybirds (Roger 1999). Predators, particularly female ladybirds, search for patches of prey in which to lay eggs that will provide their offspring with food (Kindlmann and Dixon 1993). Hence, various costs and benefits are associated with optimal foraging.

Costs are usually expressed in terms of time and energy consumed in selecting prey or the habitat of their prey and the associated risks. Prey selection is largely dependent on factors, like success in capturing prey, handling time and energy content of the prey. For instance, ladybirds attack small and intermediate sized prey as they are easy to capture. Similarly, handling time of small prey is less than that of large prey (Pervez and Omkar 2003). However, the energetic value of large prey is greater. Age and size of the ladybirds affect their foraging efficiency, for instance, old and big ladybirds are better at searching and capturing prey.

According to the assumptions of the optimal foraging theory, ladybirds should maximize their rate of successful encounters with prey per unit time. The foraging time includes time spent travelling between prey patches as well as that spent intensively searching a patch (Ferran and Dixon 1993). Hungry ladybirds resort to more intensive searching and are simultaneously less selective in their choice of prey. Ladybirds spend most time in patches where prey is abundant and/or prey is palatable (Roger 1999). Kindlmann and Dixon (2010) present a metapopulation model describing this theory by further adding components, like egg-window dynamics and within- and between-season dynamics. They conclude that the effect of predators on aphid populations is likely to be less late in the season than very early in the season, as aphid colonies are then small. Kindlmann and Dixon (1999a,b) question the effectiveness of aphidophagous ladybirds in controlling aphids as their generation time ratio (GTR) relative to that of aphids is greater than one as ladybirds develop more slowly. It is predicted that in aphid-ladybird systems, owing to the large GTR, reproduction of ladybirds should be correlated with the age of aphid colony rather than the number of aphids, and top-down regulation is weaker (Kindlmann and Dixon 2001). Results of field experiments support the GTR hypothesis, as the aphidophagous ladybirds do not have a significant negative effect on the peak numbers of the aphids (Kindlmann et al. 2015). Hence, because of their high GTR aphidophagous ladybirds are unable to regulate aphid populations in the field.

Dynamics of the Foraging Behaviour of Ladybirds

Foraging in ladybirds can be categorized broadly into three phases, *viz.* (1) location of the habitat of their prey, (2) location of their prey and (3) prey selection (Hodek 1993). These phases are driven by several factors like chemical cues, visual cues, host plant architecture, foraging deterrent pheromones, *etc*. These factors are discussed in detail below:

Chemical Cues

Hinkelman (2012) reports that foraging based on sensory cues outperforms that based on the chance encoun-

tering of resources and suggests that natural selection might favour foragers that switch to depending on sensory cues rather than encountering resources. Amongst the sensory cues, chemicals play a pivotal role in locating the habitat of their prey. Hatano et al. (2008) review this aspect and emphasize the importance of semiochemicals in prey selection by natural enemies. Similarly, Pettersson et al. (2008) give an account of the chemical stimuli important in the foraging behaviour of the seven-spot ladybird, *Coccinella septempunctata* Linnaeus. Tapia et al. (2010) also report that semiochemicals are key factors in predator-facilitation, *i.e.* presence of predators on an aphid-infested plant trigger the release of alarm pheromones by the aphids. These pheromones bring other ladybirds to the prey site that may synergistically or antagonistically affect a decrease in the aphid population. It is widely held that volatiles emitted by plants injured by herbivores are used by foraging ladybirds to locate their prey. Increasing laboratory evidence indicates that ladybirds are more attracted to damaged than undamaged host plants (Ninkovic et al. 2001; Han and Chen 2002a; Francis et al. 2004). Pare and Tumlinson (1999) are of the opinion that plants change their volatile profiles after being attacked by herbivores, particularly aphids, and thereby emit compounds synthesized de novo, which attract and guide natural enemies towards their prey.

Olfactometer experiments indicate that adults of *C. septempunctata* are attracted in greater numbers to twigs and leaves of different host plants infested with aphids than to aphids alone (Khan et al. 2017). Similarly, adults of the ladybird, *Cycloneda sanguinea* Linnaeus take less time to locate olfactometer chambers containing the aphid, *Myzus persicae* Sulzer infesting leaves of tomato, *Lycopersicon esculentum* Mill than chambers containing only *M. persicae* or leaves of tomato (Heit et al. 2008). This further indicates that foraging is largely driven by volatiles released by aphid-infested plants. The mycophagous ladybird, *Psyllobora vigintimaculata* (Say) is attracted to squash plants, *Cucurbita moschata* Duchesne, infected with powdery mildew, *Podosphaera* sp. (Tabata et al. 2011). However, aphidophagous ladybirds tend to visit undamaged plants to feed on pollen and nectar in the absence of prey (Michaud and Qureshi 2005). Similarly, certain plant volatiles are attractive for ladybirds, regardless of the plants being infested or not, and these volatiles can be used to attract ladybirds (Ninkovic and Pettersson 2003). On the contrary, adults of the ladybird *Eriopis connexa* (Germar) are not attracted to aphid infested plants in an artificial environment (Tapia et al. 2010). This probably indicates that integration of other cues might trigger or support its foraging behaviour.

Hatano et al. (2008), in their review, list chemicals from several aphid-plant complexes along with their effects on ladybirds. The soybean plant, *Glycine max* L., emits methyl salicylate when attacked by the aphid *Aphis glycines* Matsumura (Zhu and Park 2005). Applying this compound to the antennae of *C. septempunctata* results in

a positive electro antennographic (EAG) response. Similarly, benzaldehyde is emitted when the aphid, *Toxoptera aurantii* (Boyer de Fonscolombe), attacks shoots of *Camellia sinensis* L., in response to which *C. septempunctata* exhibits a positive EAG response and is attracted to the plant (Han and Chen 2002a, b). Similarly, methyl salicylate is an herbivore-induced plant volatile, which triggers ladybirds to aggregate on aphid infested plants for feeding and oviposition (Salamanca et al. 2017). These chemicals are perceived over very long distances by sensillae present on the antennae of adult ladybirds (Omkar and Pervez 2008). A few chemicals are listed below that could be used as attractants for these ladybirds and thus may be helpful in aphid biocontrol (Table 1).

Further, honeydew secreted by aphids, acts as a secondary olfactory cue in attracting predators, particularly ladybirds, to aphid prey. Artificial spraying of honeydew attracts ladybirds, *e.g. Hippodamia* sp. to aphid habitats, thereby making it useful in integrated pest management (IPM) programmes (Hagen et al. 1971; Evans and Richards 1997). Larvae of the ladybird, *H. convergens* stay longer in patches contaminated with honeydew compared to clean patches (Purandare and Tenhumberg 2012). In addition, these larvae are unable to distinguish between high and low-quality aphid honeydew. However, it also acts as an arrestant for certain predators and prolongs their searching time (Ide et al. 2007).

Foraging ladybirds also perceive kairomones released by aphids (e.g. alarm pheromones) and use them as secondary cues for prey location and thereby switch from extensive to intensive search (Francis et al. 2004, 2005). Aphids on being attacked by a ladybird larva also release *E-β-farnesene*, which attracts other conspecific larvae to attack the prey (Hemptinne et al. 2000). Cornicle secretions and cuticular chemicals of aphids are also secondary cues for foraging ladybirds (Seagraves 2009).

Visual Cues

It is an established fact that chemical cues help in locating the habitat of the prey. Further, other cues and signals are also perceived by foraging ladybirds. Amongst these cues, visual cues are considered to be the major ones. However, they are rarely mentioned in the literature where more importance is given to chemical cues. Bahlai et al. (2008) suggest that adult *H. axyridis* depend upon long-range visual cues to locate host habitats. Adult ladybirds tend to be attracted by silhouetted shapes and foliage of host plants regardless of olfactory cues. Adults of *Chilocorus nigritus* (Fabricius) prefer to forage near horizons that simulate treelines over flat horizons (Hattingh and Samways 1995). Most ladybirds prefer to forage during daytime, as they can use visual cues for finding prey. This is evident from the increased aphid consumption in daytime compared to that at night (Harmon et al. 1998). In addition, ladybirds, for instance, *C. septempunctata* consume a greater number of *A. pisum* that contrast in colour with the background. Certain ladybirds, *viz. H. convergens*, *Coleomegilla maculata* (deGeer), *H. axyridis* and *C. septempunctata*, consume more red individuals of *A. pisum* than green ones (Harmon et al. 1998). Similarly, naive adults of *H. axyridis* are more attracted to yellow than green pillars (Mondor and Warren 2000), as yellow pillars resemble stressed or young plants that are more likely to be infested with aphids (Lorenzetti et al. 1997). Most of the foraging activity of the ladybird *Propylea dissecta* (Mulsant) occurs in daytime (Mishra and Omkar 2004). However, the major life events such as mating, oviposition, hatching and moulting occur at night, which indicate the importance of visual cues that are needed for the ladybird to forage. Heit et al. (2007) did not find any difference in the foraging behaviour of adult male and female *C. sanguinea* during the morning and afternoon. However, as the day progressed, they noticed a decline in foraging probably due the fact that other activities, such as mating, are more likely to occur later in the day.

Ferran and Dixon (1993) suggest that conditioning in ladybirds affects their foraging ability. Learning from previous experience helps them to switch from extensive to intensive search. For instance, laboratory-reared *H. axyridis* have a strong affinity for pea aphids (*A. pisum*) and any sign or smell of this prey enables the predator to switch to intensive search (Ettifouri and Ferran 1993).

Locomotor Activity

The locomotor activity of predators plays a crucial role in their foraging behaviour (Bell 1990). Heit et al.

Table 1 List of the allelochemicals released by plants attacked by aphids that attract ladybirds.

Ladybird	Prey	Host Plant	Allelochemical	Reference
Coccinella septempunctata	*Aphis glycines*	*Glycine max* L.	Methyl salicylate	Zhu and Park (2005)
C. septempunctata	*Toxoptera aurantii*	*C. sinensis*	Benzaldehyde	Han and Chen (2002a)
C. septempunctata	–	–	(Z)-jasmone	Birkett et al. (2000)
C. septempunctata	–	–	(E)-β-farnesene	Al Abassi et al. (2000)
Hippodamia convergens	Eggs of *Ostrinia nubilalis* Hübner	*Vaccinium macrocarpon* Ait	Methyl salicylate	Salamanca et al. (2017)
H. convergens	*M. persicae*	–	(E)-β-farnesene	Acar et al. (2001)
A. bipunctata	*M. persicae* *A. pisum*	–	(E)-β-farnesene	Francis et al. (2004)

(2007) in their series of experiments found that locomotory activity decreases significantly when the adults encounter plant leaves infested with high or low numbers of aphids compared to when they search uninfested leaves. Ladybirds forage differently in the field compared to in the laboratory. The ladybird, *Harmonia axyridis* (Pallas) forages, attacks, kills and consumes prey at a faster rate in the field than in the laboratory (Latham and Mills 2009). Longer legs are likely to enable it to move faster (Teuscher et al. 2009). However, adults of the ladybird, *C. maculata,* attacking whitefly in greenhouses are impeded by trichomes (small hair-like outgrowths from the epidermis of a plant) whereas the smaller ladybird, *Delphastus catalinae* (Horn) is not affected by trichomes (Lucas et al. 2004). In addition, their locomotor activity is significantly greater in the afternoon than in the morning.

Certain aphids, for example the pea aphid, *A. pisum,* may detect ladybirds and respond by dropping from the plant (Losey and Denno 1998). Thus, significantly reducing the foraging efficiency of the ladybirds, which in the case of *H. axyridis* can be as much as 40% (Francke et al. 2008).

Plant Architecture

Plant architecture is important in the food choice of insect predators, particularly ladybirds, as their larvae crawl over and capture prey on the surfaces of plants (Reynolds 2011). Plant structures, particularly, their morphological features like texture, shape and size have a great effect on the foraging success of ladybirds. Plant architecture has a direct effect on the walking speed and attack rate. This also affects the host preference of ovipositing ladybirds. However, increase in the heterogeneity of plant structures decreases the foraging capacity of ladybirds. For example, larvae of the ladybird *C. septempunctata* forage less successfully for pea aphids, *A. pisum,* on highly branched varieties than on normal varieties of peas (Legrand and Barbosa 2003). Even the surface texture of plants, *i.e.* hairiness or slipperiness, affect the foraging ability of ladybird larvae. Trichomes reduce the foraging and walking speed of predators (Stavrinides and Skirvin 2003; Riddick and Simmons 2014). Similarly, waxy plants reduce the foraging success of ladybirds, for instance, larvae of *H. convergens* are more successful foraging for aphids on non-waxy cabbage than on a waxy variety (Chang et al. 2006). The effect of leaf waxes is however largely ignored in the literature. In addition, larvae of *C. septempunctata* are less effective in foraging and killing prey on foliage, which has more junctions (Legrand and Barbosa 2000).

Presence of wax on the surface of plants, especially leaves, plays a significant role in the foraging ability of ladybird larvae. Increase in surface wax reduces the walking speed and searching efficiency of coccinellid larvae, and also tends to result in the larvae loosing adhesion and falling from leaves (Rutledge and Eigenbrode 2003; Rutledge et al. 2008). The adhesion of foraging larvae depends on the texture and surface wax on leaves, for instance, the presence of crystalline epicuticular wax on the pea plant, *P. sativum* (Eigenbrode et al. 2008). A morphological study of the way *Cryptolaemus montrouzieri* Mulsant adheres to plants surfaces combined with measurements of the forces that keeps beetles attached to plant surfaces is reported by Gorb et al. (2008).

Effect of Footprints / Foraging Deterrent Pheromones

Adults and larvae of ladybirds leave trails or footprints (Mishra et al. 2012; Kumar et al. 2014a) in the form of non-volatile hydrocarbons (Magro et al. 2007), which deter other foraging ladybirds. These chemicals may be referred to as deterrent pheromones as they inhibit foraging activity (Ruzicka and Zemek 2008; Moser et al. 2010). The first instar larva of an aphidophagous ladybird, *Cycloneda limbifer* Say respond to conspecific larval tracks by avoiding or leaving such microhabitats (Ruzicka and Zemek 2008). This probably indicates that foraging larvae balance the spatial variation in the concentration of larval tracks by shifting from microhabitats with high to lower concentrations of larval tracks. Thus, in field condition, it is likely that the regulation of prey-location might be driven by the ratio between attractant and deterrent pheromone-cues. Active foraging of early instars in uninvaded or less contaminated aphid colonies reduces the risk of cannibalism or intraguild predation. In contrast, older instars search more effectively for better aphid colonies because they are less at risk. It seems that ladybird larvae optimize their distribution between aphid colonies according to the densities of both prey and larval tracks (Dixon et al. 1997; Kindlmann and Dixon 1999b).

In predatory guilds, small ladybirds are more easily deterred from foraging possibly because they are more vulnerable to intraguild predation (Kumar et al. 2014b). The fitness parameters, particularly growth-rate and conversion-efficiency, of small ladybirds even declines due to reduced foraging in habitats previously visited by other predators (Kumar et al. 2014a). In addition to deterring foraging, ladybirds' footprints also reduce the settling of herbivores, like aphids (Ninkovic et al. 2013) and psyllids (Seo et al. 2018), thereby resulting in declines in pest populations.

Issues Pertaining to the Manipulation of Ladybirds' Foraging Efficiencies

Prey density dependent searching efficiency and prey consumption by ladybirds can be best described by a functional response (Pervez and Omkar 2003, 2005; Omkar and Pervez 2004b). It is widely held that most ladybirds exhibit a Type II functional response, *i.e.* they show a negative prey density dependence response in

which their rate of prey consumption decreases with increase in prey density. It is noticeable in the field and laboratory (Pervez and Omkar 2010) that ladybirds distribute themselves spatially and temporally on plants. Thus, their effectiveness as biocontrol agents can be manipulated and certain ladybirds with different spatio-temporal distribution tendencies can be manipulated for synergistically effecting the mortality of prey populations (Omkar and Pervez 2011). This can be beneficial as there is little interference between heterospecific ladybirds attacking the same prey. However, certain risks are associated with the tandem release of large and small ladybirds in aphid infested microhabitats (Omkar et al. 2014).

Prey-preference studies indicate that ladybirds have an affinity and preference for certain prey over others (Guroo et al. 2017; Pervez and Kumar 2017). In addition, this prey-preference depends largely on the host plant, as aphids sequester host plant allelochemicals and use them as a defence against ladybirds. For instance, *Acyrthosiphon nipponicus* (Aphididae), feeds on *Paederia scandens* (Lour.) Merr. (Rubiaceae) and secretes paederoside, an iridoid glycoside and lipids from its cornicles that helps it to defend itself from *H. axyridis*, as this chemical forces the ladybird to release the aphid and flee from the aphid colony (Nishida 2014). Thus, aphids sequestering such allelochemicals become toxic and unpalatable for ladybirds, which then avoid further attacking and consuming these aphids. Hence, despite this aphid being highly preferred when raised on suitable host plants, it is avoided when raised on a toxic host. Thus, we can manage the prey preference capabilities of ladybirds by providing aphids raised on suitable and nutritious hosts rather than toxic host plants.

Conclusions

It is evident from this review that the foraging behaviour of ladybirds has been extensively investigated and modelled. However, the dynamics of searching behaviour are not well understood. Undoubtedly, mainly chemical cues guide foragers towards prey habitats. Such chemicals should be used in biocontrol programmes in order to attract foraging ladybirds to sites where prey are abundant. Visual cues are also important in facilitating the finding and selecting prey. However, this tendency greatly varies between ladybird species. Foraging deterrent pheromones are seemingly more responsible for changes in the foraging patterns of ladybirds after the prey has been located. Early instars avoid foraging in patches previously visited by predators. Furthermore, it would be risky if older instars pupate in colonies inhabited by numerous early instars, as later in their development these larvae are likely to attack the immobile defenceless pupae. Ladybirds that feed on toxic and unfamiliar prey and ignore nutritious prey during their search for prey are still

hard to explain. Advances in chemoecology have helped in our understanding of the intricacies of foraging patterns in ladybirds. However, more information regarding nature, structure and function of chemicals is needed to understand the details of foraging patterns of larvae and adult ladybirds and to implement them in biocontrol programmes.

Acknowledgements

REFERENCES

Acar EB, Medina JC, Lee ML, Booth GM (2001) Olfactory behavior of convergent lady beetles (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). Can Entomol 133: 389–397.

Al Abassi S, Birkett MA, Pettersson J et al. (2000) Response of the sevenspot ladybird to an aphid alarm pheromone and an alarm pheromone inhibitor is mediated by paired olfactory cells. J Chem Ecol 26: 1765–1771.

Bahlai CA, Welsman JA, Macleod EC, Schaafsma AW, Hallett RH, Sears MK (2008) Role of visual and olfactory cues from agricultural hedgerows in the orientation behavior of multicolored Asian lady beetle (Coleoptera: Coccinellidae). Environ Entomol 37: 973–979.

Bell WJ (1990) Searching behavior patterns in Insects. Annu Rev Entomol 35: 447–467.

Birkett MA, Campbell CAM, Chamberlain K, Guerrieri E, Hick AJ, Martin JL, Matthes M, Napier JA, Pettersson J, Pickett JA, Poppy GM, Pow EM, Pye BJ, Smart LE, Wadhams GH Wadhams LJ, Woodcock CM (2000) New roles for cis-jasmone as an insect semiochemicals and in plant defence. PNAS 97: 9329–9334.

Chang GC, Neufeld J, Eigenbrode SD, Chang GC (2006) Leaf surface wax and plant morphology of peas influence insect density. Entomol Exp Appl 119: 197–205.

Crawley MJ, Krebs JR (1992) Foraging theory. In: Crawley MJ (eds) Natural enemies. Blackwell Scientific Publications, Oxford, pp 90–114.

Dixon AFG (2000) Insect predator-prey dynamics, Ladybird beetles and biological control. Cambridge University Press, Cambridge.

Dixon AFG, Hemptinne JL, Kindlmann P (1997) Effectiveness of ladybirds as biological control agents: Patterns and Processes. Entomophaga 42: 71–83.

Eigenbrode SD, Andreas JE, Cripps MG et al. (2008) Induced chemical defenses in invasive plants: a case study with *Cynoglossum officinale* L. Biol Invasions 10: 1373–1379.

Ettifouri M, Ferran A (1993) Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* [Coccinellidae] larvae. Entomophaga 38: 51–59.

Evans EW, Richards DR (1997) Managing the dispersal of ladybird beetles (Col.: Coccinellidae): Use of artificial honeydew to manipulate spatial distributions. Entomophaga 42: 93–102.

Ferran A, Dixon AFG (1993) Foraging behaviour of ladybirds larvae (Coleoptera: Coccinellidae). Eur J Entomol 90: 383–402.

Francis F, Lognay G, Haubruge E (2004) Olfactory responses to aphid and host plant volatile releases: (E)-betafarnesene an effective kairomone for the predator *Adalia bipunctata*. J Chem Ecol 30: 741–755.

Francis F, Vandermoten S, Verheggen F, Lognay G, Haubruge E (2005) Is the (E)-beta-farnesene only volatile terpenoid in aphids? J Appl Entomol 129: 6–11.

Francke DL, Harmon JP, Harvey CT, Ives AR (2008). Pea aphid dropping behavior diminishes foraging efficiency of a predatory ladybeetle. Entomol Exp Appl 127: 118–124.

Gorb E, Voigt D, Eigenbrode SD, Gorb S (2008) Attachment force of the beetle *Cryptolaemus montrouzieri* (Coleoptera, Coccinellidae) on leaflet surfaces of mutants of the pea *Pisum sativum* (Fabaceae) with regular and reduced wax coverage. Arthropod – Plant Interact 2: 247–259.

Guroo MA, Pervez A, Srivastava K, Gupta RK (2017) Effect of nutritious and toxic prey on food preference of a predaceous ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae). Eur J Entomol 114: 400–406.

Hagen JS, Sawall EF Jr, Tassan RL (1971) Use of food sprays to increase effectiveness of entomophagous insects. Proc. Tall Timbers Conference on Ecological Animal Control By Habitat Management. Feb. 26–28, 1970, Tallahassee, Florida, USA, Vol 2: 59–81.

Han BY, Chen ZM (2002a) Behavioral and electrophysiological responses of natural enemies to synomones from tea shoots and kairomones from tea aphids, *Toxoptera aurantii.* J Chem Ecol 28: 2203–2219.

Han BY, Chen ZM (2002b) Composition of the volatiles from intact and mechanically pierced tea aphid-tea shoot complexes and their attraction to natural enemies of the tea aphid. J Agr Food Chem 50: 2571–2575.

Harmon JP, Losey JE, Ives AR (1998) The role of vision and color in the close proximity foraging behavior of four coccinellid species. Oecologia 115: 287–292.

Hatano E, Kunert G, Michaud JP, Weisser WW (2008) Chemical cues mediating aphid location by natural enemies. Eur J Entomol 105: 797–806.

Hattingh V, Samways MJ (1995) Visual and olfactory location of biotopes, prey patches, and individual prey by the ladybeetle *Chilocorus nigritus*. Entomol Exp Appl 75: 87–98.

Heit GE, Sardoy P, Cohen GR, Mareggiani G (2007) Locomotor activity of *Cycloneda sanguinea* (Coleoptera: Coccinellidae) exposed to volatile semiochemicals and to direct contact with the odour source. Rev Soc Entomol Argent 66: 197–203.

Heit GE, Cohen GR, Mareggiani G (2008) Impact of odor signals on *Cycloneda sanguinea* (Coleoptera: Coccinellidae) searching behavior. Cien Inv Agr 35: 205–210.

Hemptinne JL, Gaudin M, Dixon AFG, Lognay G (2000) Social feeding in ladybird beetles: adaptive significance and mechanism. Chemoecology 10: 149–152.

Hinkelman TM (2012) Foraging Challenges: Unsuitable Prey and Limited Information. Ph.D. Thesis, School of Biological Sciences. University of Nebraska, Lincoln.

Hodek I (1993) Habitat and food specificity in aphidophagous predators (a review). Biocontrol Sci Technol 3: 91–100.

Hodek I, Evans EW (2012) Food relationship. In Hodek I, van Emden HF, Honek A (eds) Ecology and behaviour of ladybird beetles (Coccinellidae). Wiley-Blackwell, pp 141–274.

Hodek I, van Emden HF, Honek A (2012) Ecology and behavior of the ladybird beetles (Coccinellidae). Wiley-Blackwell, Oxford, United Kingdom.

Ide T, Suzuki N, Katayama N (2007) The use of honeydew in foraging for aphids by larvae of the ladybird beetle, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Ecol Entomol 32: 455–460.

Khan AA, Khan MA, Afzal M (2017) Olfactory response of ladybird beetle, *Coccinella septempunctata* L. (Coccinellidae: Coleoptera) towards aphids and their host plants. Pak J Zool 49: 1539–1541.

Kindlmann P, Dixon AFG (1993). Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. Eur J Entomol 90: 443–450.

Kindlmann P, Dixon AFG (1999a) Generation Time Ratios-Determinants of Prey Abundance in Insect Predator–Prey Interactions. Biol Cont 16: 133–138.

Kindlmann P, Dixon AFG (1999b) Strategies of aphidophagous predators: lessons for modelling insect predator–prey dynamics. J Appl Ent 12: 286–288.

Kindlmann P, Dixon AFG (2001) When and why top-down regulation fails in arthropod predator-prey systems. Basic Appl Ecol 2: 333–340.

Kindlmann P, Dixon AFG (2010) Modelling Population Dynamics of Aphids and Their Natural Enemies. In: Aphid biodiversity under environmental change: patterns and processes. Proc 7th Intl Symp Aphids. Fremantle, Australia. pp 1–20.

Kindlmann P, Yasuda H, Kajita Y, Sato S, Dixon AFG (2015) Predator efficiency reconsidered for a ladybird-aphid system. Frontiers Ecol Evol 3: 1–5.

Kumar B, Mishra G, Omkar (2014a) Larval and female footprints as feeding deterrent cues for immature stages of two congeneric ladybird predators (Coleoptera: Coccinellidae). Bull Ent Res 104: 652–660.

Kumar B, Bista M, Mishra G, Omkar (2014b) Stage specific consumption and utilization of aphids, con-specific and hetero-specific eggs by two species of Coccinella (Coleoptera: Coccinellidae). Eur J Entomol 111: 363–369.

Latham DR, Mills NJ (2009) Quantifying insect predation: a comparison of three methods for estimating daily per capita consumption of two aphidophagous predators. Environ Entomol 38: 1117–1125.

Legrand A, Barbosa P (2000) Pea aphid (Homoptera: Aphididae) fecundity, rate of increase, and within-plant distribution unaffected by plant morphology. Environ Entomol 29: 987–993.

Legrand A, Barbosa P (2003) Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Environ Entomol 32: 1219–1226.

Lorenzetti F, Arnason JT, Philogene BJR, Hamilton RI (1997) Evidence for spatial niche partitioning in predaceous aphidophaga: Use of plant colour as a cue. Entomophaga 42: 49–56.

Losey JE, Denno RF (1998) Positive predator- predator interactions: enhanced predation rate and synergistic suppression of aphid populations. Ecology 79: 2143–2152.

Lucas E, Labreque C, Coderre D (2004) *Delphastus catalinae* and *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae) as biological control agents of the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). Pest Management Sci 60: 1073–1078.

Magro A, Tene JN, Bastin N, Dixon AFG, Hemptinne JL (2007) Assessment of patch quality by ladybirds: relative response to conspecific and heterospecific larval tracks a consequence of habitat similarity? Chemoecology 17: 37–45.

Michaud JP, Qureshi JA (2005) Induction of reproductive diapause in *Hippodamia convergens* (Coleoptera: Coccinellidae) hinges on prey quality and availability. Eur J Entomol 102: 483–487.

Mishra G, Omkar (2004) Diel rhythmicity in certain life events of ladybird, *Propylea dissecta* (Mulsant). Biol Rhythm Res 35: 269–276.

Mishra G, Singh N, Shahid M, Omkar (2012) Effect of presence and semiochemicals of conspecific stages on oviposition by ladybirds (Coleoptera: Coccinellidae). Eur J Entomol 109: 363–371.

Mondor EB, Warren JL (2000) Unconditioned and conditioned responses to colour in the predatory coccinellid, *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur J Entomol 97: 463–467.

Moser SE, Haynes KF, Obrycki JJ (2010) Behavioral response to larval tracks and the influence of tracks on intraguild scavenging by coccinellid larvae. J Insect Behav 23: 45–58.

Murdie G (1971) Simulation on the effects of predators/ parasite models on prey/host spatial distribution. In Patil GP, Pielou EC, Waters WE (eds) Statistical Ecology 1. Pennsylvania State University Press, Harrisburg, pp 215–223.

Ninkovic V, Al Abassi S, Pettersson J (2001) The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. Biol Cont 21: 191–195.

Ninkovic V, Feng Y, Olsson U, Petterson J (2013) Ladybird footprints induce aphid avoidance behavior. Biol Control 65: 63–71.

Ninkovic V, Pettersson J (2003) Plant/plant communication supports searching behaviour of the sevenspotted ladybird, *Coccinella septempunctata* (L.)? Oikos 100: 65–70.

Nishida R (2014) Chemical ecology of insect-plant interactions: ecological significance of plant secondary metabolites. Biosci Biotech Biochem 78: 1–13.

Omkar, Mishra G, Kumar B, Singh N, Pandey G (2014) Risks associated with tandem release of large and small ladybirds (Coleoptera: Coccinellidae) in heterospecific aphidophagous guilds. Can Entomol 146: 52–66.

Omkar, Pervez A (2004a) Predaceous coccinellids in India: Predator-prey catalogue. Oriental Insects 38: 27–61.

Omkar, Pervez A (2004b) Functional and numerical responses of *Propylea dissecta* (Mulsant) (Col., Coccinellidae). J Appl Entomol 128: 140–146.

Omkar, Pervez A (2008) Antennal sensillae of an aphidophagous ladybird, *Propylea dissecta*. J Appl Biosci 34: 168–171.

Omkar, Pervez A (2011) Functional Response of two aphidophagous ladybirds searching in tandem. Biocont Sci Tech 21: 101–111.

Omkar, Pervez A (2016) Ladybird Beetles. In: Omkar (ed) Ecofriendly Pest Management for Food Security. Academic Press Chapter 9: 281–310.

Pare PW, Tumlinson JH (1999) Plant volatiles as a defense against insect herbivores. Plant Physiol 121: 325–331.

Pervez A, Kumar R (2017) Preference of the aphidophagous ladybird, *Propylea dissecta* for two species of aphids reared on toxic host plants. Eur J Environ Sci 7: 130–134.

Pervez A, Omkar (2003) Predation potential and handling time estimates of a generalist aphidophagous ladybird, *Propylea dissecta*. Biol Mem 29: 91–97.

Pervez A, Omkar (2004) Prey dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). Biocon Sci Technol 14: 385–396.

Pervez A, Omkar (2005) Functional response of coccinellid predators: An illustration of a logistic approach. J Insect Sci 5: 1–6.

Pervez A, Omkar (2010) Innovations in the aphid biocontrol programme using predaceous ladybirds. Proc Nat Symp Modern Approaches to Insect Pest Manag (March 26–27, 2010), p. 95–105.

Pettersson J, Ninkovic V, Glinwood R, Al Abassi S, Birkett M, Pickett J, Wadhams L (2008) Chemical stimuli supporting foraging behaviour of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae): volatiles and allelobiosis. Appl Entomol Zool 43: 315–321.

Purandare SR, Tenhumberg B (2012) Influence of aphid honeydew on the foraging behaviour of *Hippodamia convergens* larvae. Ecol Entomol 37: 184–192.

Reynolds P (2011) The effects of plant gross morphology on the foraging efficiencies of generalist predators. M.Sc. Thesis, University of Waterloo.

Riddick EW (2017) Identification of conditions for successful aphid control by ladybirds in greenhouses. Insects 8, 38, doi: 10.3390/insects8020038.

Riddick EW, Simmons AM (2014) Do plant trichomes cause more harm than good to predatory insects? Pest Manag Sci 70: 1655–1665.

Roger C (1999) Mechanisms of prey selection in the ladybeetle *Coleomegilla maculata* Lengi Timb. (Coleoptera: Coccinellidae). Ph.D. Thesis, Department of Natural Resource Sciences, Macdonald campus of McGill University, Montréal Canada.

Rutledge CE, Eigenbrode SD (2003) Epicuticular wax on pea plants decreases instantaneous search rate of *Hippodamia convergens* larvae and reduces attachment to leaf surfaces. Can Entomol 135: 93–101.

Rutledge CE, Eigenbrode SD, Ding H (2008) A plant surface mutation mediates predator interference among ladybird larvae. Ecol Entomol 33: 464–472.

Ruzicka Z, Zemek R (2008) Deterrent effects of larval tracks on conspecific larvae in *Cycloneda limbifer*. Biol Cont 53: 763–771.

Salamanca J, Souza B, Lundgren JG, Rodriguez-Saona C (2017) From laboratory to field: electro-antennographic and behavioral responsiveness of two insect predators to methyl salicylate. Chemoecology 27: 51–63.

Seagraves MP (2009) Lady beetle oviposition behavior in response to the trophic environment. Biol Cont 51: 313–322.

Seo M, Rivera MJ, Stelinski LL (2018) Trail chemicals of the Convergens ladybird beetle, *Hippodamia convergens*, reduce feeding and oviposition by *Diaphorina citri* (Hemiptera: Psyllidae) on Citrus Plants. J Insect Behav 31: 298–308.

Stavrinides MC, Skirvin DJ (2003) The effect of chrysanthemum leaf trichome density and prey spatial distribution on predation of *Tetranychus urticae* (Acari: Tetranychidae) by *Phytoseiulus persimilis* (Acari: Phytoseiidae). Bull Ent Res 93: 343–350.

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton.

Tabata J De Moraes CM Mescher MC (2011) Olfactory cues from plants infected by powdery mildew guide foraging by a mycophagous ladybird beetle. PLoS One 6: 1–6.

Tapia DH, Morales F, Grez AA (2010) Olfactory cues mediating prey-searching behaviour in interacting aphidophagous predators: are semiochemicals key factors in predator-facilitation? Ent Exp Appl 137: 28–35.

Teuscher M, Brandl M, Traxel V, Brandl R (2009) Allometry between leg and body length of insects: lack of support for the size-grain hypothesis. Ecol Entomol 34: 718–724.

Wiens JA (1976) Population Responses to Patchy Environments. Annu Rev Ecol Syst 7: 81–120.

Zhu JW, Park KC (2005) Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. J Chem Ecol 31: 1733–1746.

INCREASING CONCENTRATION OF DEICING SALT IN SOILS IN THE BAVARIAN FOREST NATIONAL PARK

ZDENKA KŘENOVÁ[1,2,*], VLADIMÍR ZÝVAL[3], VLADIMÍR ZÝVAL JR.[3], and ZDEŇKA CHOCHOLOUŠKOVÁ[4]

[1] Global Change Research Centre AS CR, v.v.i., Bělidla 4a, CZ-60200 Brno, Czech Republic
[2] Charles University, Faculty of Sciences, Benátská 2, CZ-12900 Prague, Czech Republic
[3] GeoVision s.r.o., Brojova 2113/16, 326 00 Plzeň 2 – Slovany, Czech Republic
[4] Department of Biology, Faculty of Education, University of West Bohemia in Plzeň, Univerzitní 8, 306 14 Plzeň, Czech Republic
* Corresponding author: zd.krenova@gmail.com

ABSTRACT

The negative effects of applying deicing salts to ecosystems are well documented for many countries. Most chemical transport from roads occurs in stormwater runoff through or over soil. Runoff pollutants alter soil chemistry, may be absorbed by plants and affect stream ecosystems, where they are dispersed and diluted over considerable distances. There was little detailed knowledge of the effects of deicing salts on ecosystems in the Bavarian Forest NP until 2011, when nine permanent sites were established along the main road in the eastern part of the NP. Soil samples were collected from four of these permanent sites in 2012, 2015 and 2018 and analysed by a certified laboratory. The results of soil chemical analysis were used to compare sites and samples from years 2012, 2015 and 2018. Our research confirmed the increasing concentrations of Na^+ and Cl^- ions in ecosystems in the Bavarian Forest NP. The highest concentrations of Na^+ and Cl^- ions were recorded in samples from sites # 4 and 5, which are located only several meters from the bank of the Grosse Ohe River. These concentrations were more than ten times higher than in samples from sites where deicing salt was not used. Amphibians, water insects and other extremely sensitive species and habitats occur in this part of the Bavarian Forest NP and are probably suffering from increasing salinity of their habitats. More research focusing on a better understanding of the spread of deicing salt in the ecosystem together with improving road maintenance technologies are need in order to improve the situation.

Keywords: ecosystem contamination; national park; road salting; soil chemistry

Introduction

Roads are a widespread and increasing feature of most landscapes. There are many scientific publications that support the general conclusion that roads have negative effects on the biotic integrity of both terrestrial and aquatic ecosystems (e.g. Trombulack and Frissell 1999). Roads of all kinds have several general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behaviour, alteration of the physical environment including habitat fragmentation, alteration of the chemical environment, spread of exotics and increase in use of areas by humans (van der Ree et al. 2015).

The negative effects of applying deicing salts to ecosystems are well known and documented for many countries, both in urban and natural areas (Findlay and Kelly 2011). Most chemical transport from roads occurs in stormwater runoff through or over soil (Forman and Alexander 1998). Runoff pollutants alter soil chemistry, may be absorbed by plants and affect stream ecosystems, where they are diluted and dispersed over considerable distances (Gilson et al. 1994; Yousef et al. 1985). Deicing salt and heavy metals are the two main categories of pollutants in road runoff. The primary deicing agent, NaCl, corrodes vehicles and bridges, contaminates drinking water supplies and is toxic to many species of plants, fish and other aquatic organisms. Sometimes calcium magnesium acetate (CMA) is used as it is a more effective deicer, less corrosive, less mobile in soil, biodegradable and less toxic to aquatic organisms (National Research Council 1991; Ostendorf et al. 1993; Forman and Alexander 1998). Also, CaCl used to decrease dust may inhibit amphibian movement (eMaynadier and Hunter 1995). Airborne NaCl from snow ploughing of roads may also cause injury to the leaves of trees up to 120 m from a road, especially downwind and downslope (Hofstra and Hall 1971; Czerniawska-Kusza 2004; *personal observation too*).

Sodium accumulation in soils, mainly within 5 m of a road, alters soil structure, which affects plant growth and plant species composition. Deicing agents tend to increase the mobility of chemical elements in soil, such as heavy metals (by NaCl) and Na, Cl, Ca and Mg (by CMA) (Amrhein et al. 1992; Bäckström et al. 2004). This process facilitates contamination of groundwater, aquifers and streams (Cunningham et al 2007). Because of dilution, the chemical effects of road runoff on surface water ecosystems may be primarily confined to small streams, particularly those adjacent to roads (Fennessey 1989).

In cold regions, deicing salts applied to roads are a major contributor to local and regional contamination, while salts from water softeners and septic systems are less important. There is emerging evidence that NaCl, the most often used deicing salt, contrary to what was previously thought is not transported rapidly through the soil and groundwater (Mason et al. 1999; Bryson and Barker 2002; Godwin et al. 2003). The retention via

several mechanisms means that the flushing-out of winter-applied salts does not occur, and high concentrations may be present during summer when biological activity is high. This can affect the living conditions of water organisms, especially their most sensitive developmental stages. Several studies document the negative cumulative effects on amphibians breeding in vernal pools near roads (Karraker et al. 2008). Denoel et al. 2010 report no effects on mortality or growth of amphibians but a reduction in the speed of movement of tadpoles at sites where there is a high concentration of salt. High concentrations of salt affect competition and predation and also cause significant changes in plant (i.e. Angold 1997; Richburg et al. 2001; Wrobel et al. 2006) and soil invertebrate communities (Rusek and Rusek 1999).

In some countries, for example the Czech Republic, the application of deicing salts to roads in protected areas is prohibited by law. In the Šumava National Park, the nearest trans-boundary partner of the Bavarian Forest NP, there are special exceptions for several main roads, where deicing salts are applied but only when particular conditions prevail and are monitored (Zýval et al. 2015, 2018). The monitoring of the effects of deicing salt on ecosystems in the Šumava NP was started in 2003, but the first monitoring was carried out already in the 1990s.

Deicing salt is regularly applied along the "Nationalparkstrasse" road, the main road in the eastern part of the Bavarian Forest NP, however nothing was known about the effects of this until 2011 when the first monitoring was started (Křenová et al. 2012). A monitoring program was prepared (Křenová 2011) and a standard monitoring design implemented (Zýval et al. 2015). Together with the monitoring of vegetation (i.e. phytoindication), soil structure and soil chemistry were also investigated at permanent sites along the "Nationalparkstrasse" road.

In this paper, we present results of soil chemical analysis, compare data collected in 2012, 2015 and 2018, and discuss trends in contamination of ecosystems in the NP.

Methodology

Study area

The Bavarian Forest National Park (24,235 ha, established 1970) is located in the German part of the Bohemian Forest and is contiguous with similar forests in the Czech Republic, where the Šumava National Park is located. These two national parks share a forest landscape, which is one of the largest in Central Europe and covers the highest ridges of the low mountain range that form the watershed between the Danube and Elbe catchment areas. About 98% of the Bavarian Forest NP is covered by forest (Elling et al. 1987) and peat bogs are the second most important habitat in this area.

This region is characterized by montane and high montane areas within a vertical range of approximately

800 m (from 650 m to 1420 m a. s. l.). At a larger scale, the Bavarian Forest is in the temperate zone and subject to both Atlantic and continental influences. The total annual precipitation is between 1200 and 1800 mm depending on altitude. Annual mean air temperature varies between 5.1 °C in the valleys, 5.8 °C on hillsides and 3.8 °C in the high montane zones (Noack 1979; Bässler 2004). Geologically, the Bavarian Forest is on the southwestern part of the Bohemian Massif (Variscian basement), which consists mainly of granite and gneiss. Consequently, soils are acidic, sandy and loamy (particularly brown earths and podsols) and partly covered with rocks. At all altitudes, but especially in the valleys, there is characteristically a persistent or intermittent water table in both mineral and organic soils (Bässler et al. 2009).

"Nationalparkstrasse", a main road in the eastern part of the Bavarian Forest NP, was constructed soon after opening the Bavarian Forest NP in 1970s. This road runs through the south-eastern edge of the Bavarian Forest NP and connects the main visitor facilities, including the main visitor centre and canopy trail. The road is open all year and frequently used by private cars and 'Igle Busses', i.e. green buses organized by the Bavarian Forest NP Authority. Local people also often use this road. It is the only usable road for some of them for travelling to their jobs or schools. The road is maintained by the Landratsamt Freyung-Grafenau office, which confirmed applying deicing salt usually from late November to April. The frequency and amount of deicing salt depends on climatic conditions and varies from 10 g/m² to 40 g/m². They said that only rock salt NaCl is used for deicing roads in the Bavarian Forest NP.

A monitoring of the effect of deicing salt along this road was agreed with the Bavarian Forest NP Authority

Table 1 The study sites and their geographical characteristics. The sites from which soil samples were collected are in bold.

Site #	Name	GPS	Altitude m a.s.l.	Salt +/–
1	Mauth – main road	N48 53.118 E13 34.522	772	+
2	Mauth – control	N48 53.218 E13 34.551	773	–
3	**Racheldiensthütte**	**N48 55.401 E13 24.644**	**773**	**–**
4	**Grosse Ohe – west**	**N48 55.416 E13 24.862**	**765**	**+**
5	**Grosse Ohe – east**	**N48 55.406 E13 24.817**	**764**	**+**
6	Waldhäuser	N48 56.237 E13 27.288	847	+
7	Grosse Filz	N48 55.338 E13 25.210	777	+
8	**Guglöd**	**N48 55.388 E13 25.106**	**769**	**+**
9	Atlschönau	N48 54.664 E13 27.977	748	+

and the first survey of the study area was done during the summer of 2011. "*Nationalparkstrasse*" and two roads running tangentially to this road to Waldhäuser and Racheldienesthütte were included in this project. The road to Waldhäuser is also treated with deicing salt, while the road to Racheldienesthütte is closed for public transport and only infrequently treated.

Data collection and analyses

Nine permanent sites were established in the study area, seven of which were located along roads where deicing salts were regularly applied (the main road *Nationalparkstrasse* and the road to Waldhäuser). Two of the study sites were along roads that were not salted and they were used as control sites. All sites were provided

Table 2 Soil profiles and their characteristics at sites # 3, 4, 5 and 7. Sample 1 was located five meters and sample 2 ten meters from the edge of the road. Samples (in bold) were collected in periodically flooded depressions along the Grosse Ohe River at sites # 4 and 5.

	Sample	Depth (m)	Soil characteristics
Site # 3	1	0–0.05	organogenic soil
		0.05–0.3	organogenic soil with lower proportion of silk
		>0.3	organogenic soil with lower proportion of silk and sand
	2	0–0.05	organogenic soil
		0.05–0.3	organogenic soil with lower proportion of silk
		>0.3	organogenic soil with lower proportion of silk and sand
Site # 4	1	0–0.05	sandy soil, grey-black, humic
		0.05–0.3	loamy sand soil, grey, locally red spots, lower more clay – flooded alluvium
		>0.3	grey-black clay
	2	0–0.05	sandy soil, grey-black, humic
		0.05–0.3	shallow grey sandy clay,
	3	0–0.05	sandy soil, grey-black, humic, periodically flooded local depression
		0.05–0.3	shallow grey sandy clay,
Site # 5	1	0–0.3	grey-green sandy soil, red-rusty glay; with paragneiss debris – probably periodically flooded alluvium
		>0.3	gravel & stones
	2	0–0.2	sandy soil, black to grey-black, humic
		0.2–0.3	grey stony sand – periodically flooded alluvium & buried humic horizon
	3	0–0.3	grey-green sandy soil, red-rusty glay; with paragneiss debris – periodically flooded depression
		>0.3	gravel & stones
Site # 8	1	0–0.05	grey-brown clay, slightly humic, partly decomposed litter
		0.05–0.4	strongly sandy soil, brown, with paragneiss debris
		>0.5	permanently waterlogged
	2	0–0.05	grey-brown clay, slightly humic, partly decomposed litter
		0.05–0.4	strongly sandy soil, red-brown, paragneiss debris

Table 3 Descriptive statistics of 60 soil samples collected in years 2012, 2015 and 2018.

Variable	Extraction	Valid N	Mean	Minimum	Maximum	Std. Dev.
Ca^{2+} [mg/kg]	Moehlich II	60	957.64	0.40	5180.00	1316.21
K^+ [mg/kg]	Moehlich II	60	112.95	11.90	312.50	68.01
Mg^{2+} [mg/kg]	Moehlich II	60	227.56	3.50	1950.00	414.37
Na^+ [mg/kg]	Moehlich II	60	281.79	0.40	1280.00	300.78
Na^+ [mg/l]	water	60	12.48	1.00	60.30	13.89
Cl^- [mg/l]	water	60	14.21	0.90	141.00	22.96
conductivity [mS/m]		60	10.00	1.67	58.50	10.04
pH (water)		60	6.25	4.66	7.90	0.69
pH (KCl)		60	3.88	3.00	6.50	0.54

with blue permanent markers, had their GPS positions recorded (Table 1) and photographed.

Two five-meters long transects were established at each site in August 2011 in order to identify the plants occurring there. The species occurrences and their salt-tolerance were repeatedly studied (Křenová et al. 2012; Zýval et al. 2015).

Soil conditions were recorded at all these sites at distances of 5 and 10 meters from the road edge (Table 2). Samples of soil were collected at distances of 5 and 10 meters from the road edge at four sites (Site # 3, 4, 5 and 8) in 2012, 2015 and 2018. The soil samples were collected from the upper (0 m to −0.10 m) and lower soil horizons (> −0.10 m) at four points and then samples from each soil horizon mixed for each site.

Each soil sample was marked with a specific code. The first digit was the site number, the second digit was the distance from the edge of the road (1 = 5 m, 2 = 10 m) and the third digit was the horizon of soil sampled (1 = upper 10 cm, 2 = deeper than 10 cm).

In 2012, 2015 and 2018, the mixed soil samples for each site were analysed by a certified laboratory in Klatovy (LABTECH Brno s.r.o – Laboratory Klatovy) and the following parameters measured:

- after water extraction: pH_{H20}, Na^+, Cl^-, conductivity;
- Moehlich II: Ca^{2+}, Mg^{2+}, K^+, Na^+;
- pH_{KCl}.

We used the analysis of variation in STATISTICA 12 (Anonymous 2012) to compare the study sites and determine the effect of distance from the edge of the road and soil sample horizon on the concentration of Na^+ and Cl^- ions. We also tested for trends over time and compared samples from 2012, 2015 and 2018 in Repeated Measurement in Split-plot ANOVA in STATISTICA 12. Logarithmic transformation $\log(x + 1)$ was used to standardize the data.

Results

A total of sixty samples collected in 2012, 2015 and 2018, were analysed. A set of twenty samples were collected and sent for laboratory analyses each year (Table 3).

The sites studied differed significantly in all variables analysed, except pH_{H20} (ANOVA, $p < 0.05$; Fig. 1). Site # 3 had the highest concentrations of cations (Ca^{2+}, Mg^{2+}, K^+) and the lowest ions from deicing salt (Na^+, Cl^-). The highest concentrations of the salt ions (Na^+, Cl^-) were recorded in samples from site # 4 and only slightly lower concentrations in samples from site # 5. The lowest concentrations of cations (Ca^{2+}, Mg^{2+}, K^+) and low concentrations of the salt ions (Na^+, Cl^-) were recorded in the samples from site # 8.
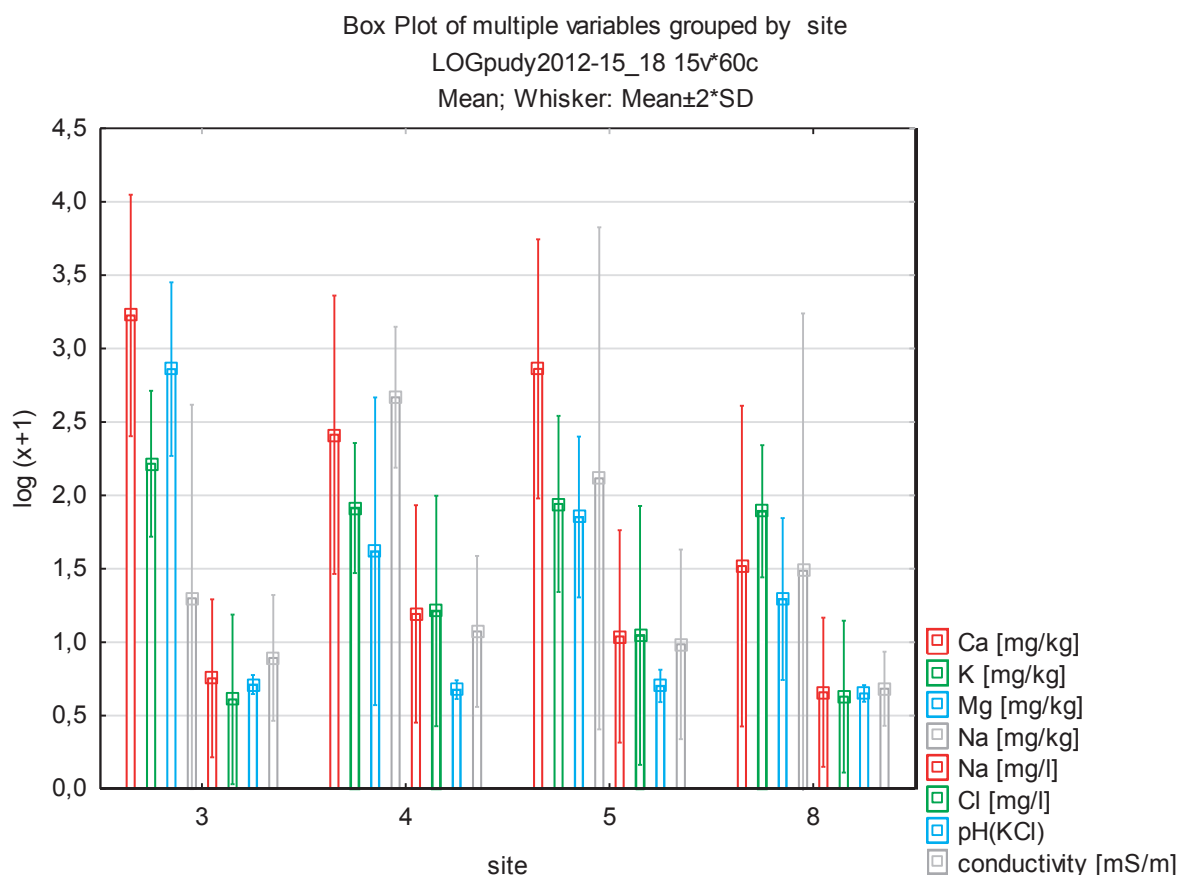
Fig. 1 Four study sites differed significantly in all the variables analysed, except pH_{H20} (ANOVA, $p < 0.05$). Mean and standard deviation bars are shown. Variables in [mg/l] were analysed after water extraction and variables in [mg/kg] were analysed after Moehlich II extraction.

There were no significant differences between samples from upper and lower soil horizons. Only slightly lower concentrations of all variables measured were recorded in samples from the low horizon. Distance of the samples from the road edge significantly affected the variables. The samples collected at a distance 10 m from the road edge had significantly higher conductivities and concentrations of Na^+, Cl^-, Ca^{2+} and Mg^{2+} ions than those collected at a distance 5 m from the road edge (ANOVA, $p < 0.05$).

There were trends in the concentration of the salt ions (Na^+, Cl^-) over time as the concentration of Na^+ ions detected after water extraction significantly increased during the study period 2012–2015–2018 (ANOVA, $p < 0.05$), while Cl^- and Na^+ ions detected after Moehlich II extraction did not change significantly. At all sites, there were similar concentrations of these two ions detected after Moehlich II extraction during the study period, with a slight decrease in 2015 and increase in 2018 (Fig. 2). There was also a statistically significant effect of site × year interaction (ANOVA, $p < 0.05$; Fig. 3). Concentrations of salt ions (Na^+, Cl^-) were highest in samples from sites # 4 and 5, both close to the Grosse Ohe River, but there were no clear trends. Chloride ions (Cl^-) increased in samples from sites # 4 and 5 and decreased in those from sites # 3 and 8 between 2012 and 2018. Also

concentrations of Na^+ ions, detected after both water and Moehlich extractions, increased in samples from sites # 4 and # 5 during the study period. Whilst the concentration of Na^+ ions continuously increased in samples from site # 4 during the study period, the concentrations of Na^+ ions steeply increased from 2012 to 2015 and later slightly decreased in those from site # 5. However, concentrations of Na^+ ions in samples collected in 2018 are higher than in those collected in 2012.

There was a decrease in the concentrations of Cl^- and Na^+ ions (Moehlich extraction) over time but after water extraction and the changes in concentrations of Na^+ ions were not obvious in the sample from site # 8.

The lowest concentrations of salt ions (Na^+, Cl^-) were recorded in samples from site # 3, where there were no trends but the largest variation in concentrations occurred during the study period.

Conclusions and Recommendation

In years 2012, 2015 and 2018, soil samples were collected in the eastern part of the Bavarian Forest NP and analysed in order to better understand the process of contamination of the national park ecosystems by deicing salt. We compared study sites and used Design of
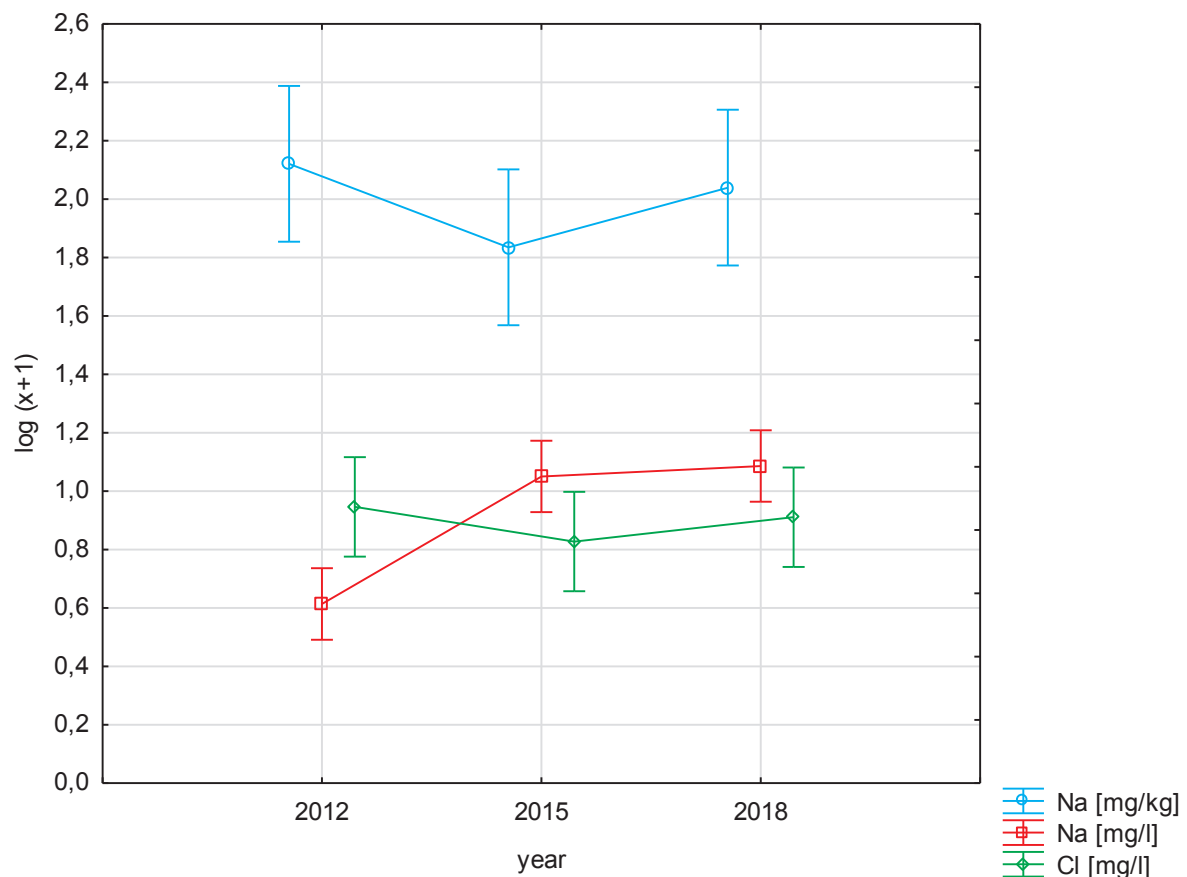
Fig. 2 Concentrations of salt ions (Na^+, Cl^-) recorded over time. Concentration of Na^+ ions detected after water extraction significantly increased during the study (ANOVA, $p < 0.05$). Vertical bars denote 0.95 confidence intervals. Variables in [mg/l] were analysed after water extraction and variables in [mg/kg] after Moehlich II extraction. Cl^- and Na^+ ions detected after Moehlich II extraction did not differ significantly.

Repeated Measurement in Split-plot ANOVA to analyse changes in the concentrations of the salt ions (Na^+, Cl^-) over time.

We found that the soil samples collected from the different sites differed significantly in their chemical parameters. The highest concentrations of Na^+ and Cl^- ions were recorded in samples from sites # 4 and 5, which are both located only several meters from the bank of the Grosse Ohe River, and water from the road is the main transport vector to the river of Na^+ and Cl^- ions. Much higher concentrations of Na^+ and Cl^- ions were recorded in samples collected 10 meters than 5 meters from the road edge. It is assumed that this because the location is subject to long-term contamination due to the accumulation of water there from melting snow. Site # 3 is located along a local road to Racheldiensthütte, which is not treated with deicing salt. This study site is about 200 meters from the "*Nationalparkstrasse*" road and also located close to the Grosse Ohe River. This study site was originally established as a control for two nearby sites # 4 and 5, but differences in soil type and water regime limit the "control" role of site # 3.

Site # 3 has anthropogenic soil with a higher proportion of cations (Ca^{2+}, Mg^{2+}, K^+) and is at a greater distance from the Grosse Ohe River, which results in a lower flushing of soil sediments than at sites # 4 and 5. These

differences may account for the high variability in the data recorded over the three years and no obvious trends in the concentrations of Na^+ and Cl^- ions recorded in samples from site # 3. Following this experience, we propose to keep site # 3 as a "control" site, but only for monitoring vegetation, and establish a new "background" study site for monitoring soil chemistry. The new study site should be closer to the Grosse Ohe River, where the soil has similar characteristics and water regime, at least 200 m above the bridge on the "*Nationalparkstrasse*" road. Site # 8 is located where the "*Nationalparkstrasse*" road passes through young dense forest. Aerosol, dust and snow ploughing are the main vectors of Na^+ and Cl^- ions, while ground water is not so important at this site. Defoliation of trees close to the edge of the road and contamination of the soil will also probably increase in the future.

This research confirms that there has been an increase in the concentrations of Na^+ and Cl^- ions in ecosystems in the Bavarian Forest NP as a result of applying deicing salt to roads. The highest concentrations, more than ten times higher than at a site where deicing salt was not applied, were recorded only several meters from the bank of the Grosse Ohe River. Amphibians, water insects and other extremely sensitive species and habitats occur in this part of the Bavarian Forest NP and are probably
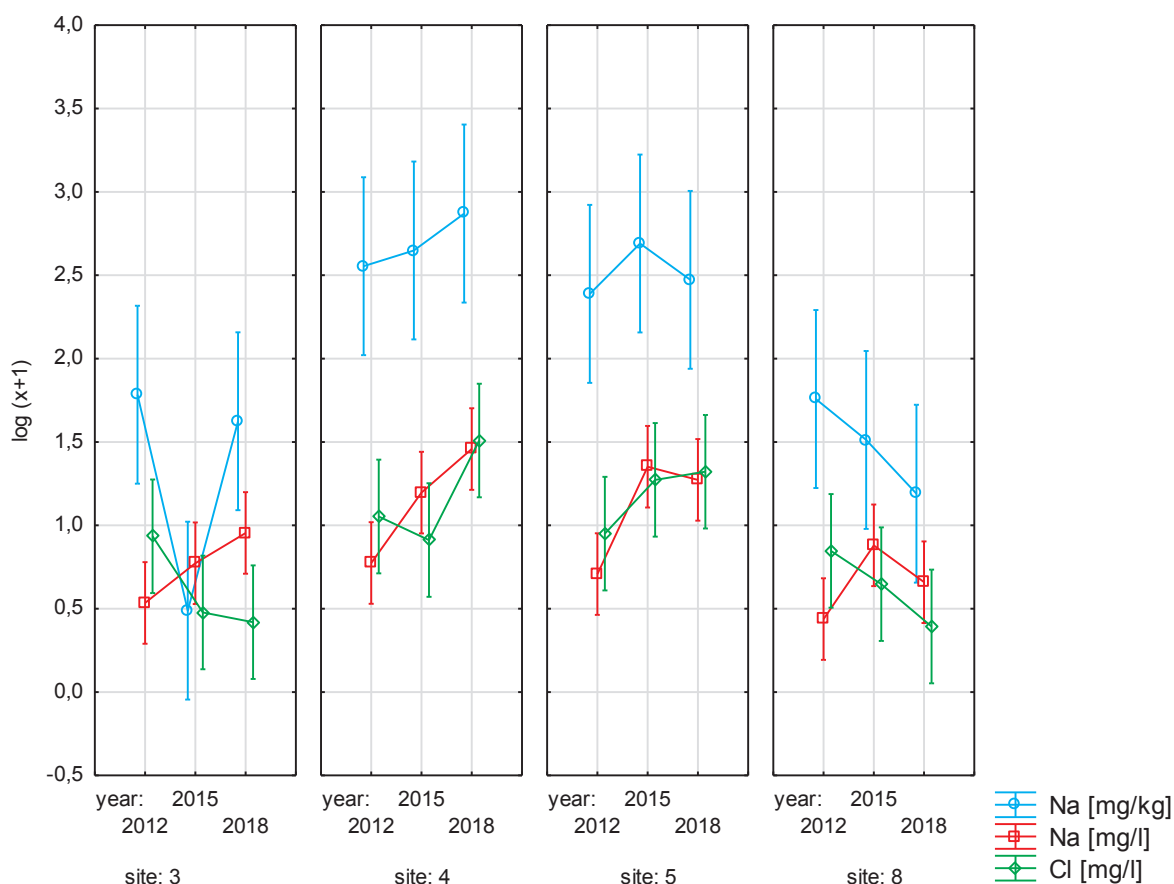
Fig. 3 Concentrations of the salt ions (Na^+, Cl^-) in samples from four study sites over time. There was a statistically significant effect of the site x year interaction (ANOVA, $p < 0.05$). Vertical bars denote 0.95 confidence intervals. Variables in [mg/l] were analysed after water extraction and variables in [mg/kg] after Moehlich II extraction. Cl^- and Na^+ ions detected after Moehlich II extraction did not differ significantly.

adversely affected by the increasing salinity in their habitats. There is a need for more research focusing on a better understanding of effects of using deicing salt in this ecosystem together with using less damaging methods for maintaining the roads.

We established permanent monitoring sites along the "*Nationalparkstrasse*" road several decades after deicing salt was first used at this location. Therefore, we lack baseline data for soil variables. Due to the lack of this data it is difficult to distinguish the effects on the ecosystem and microhabitats of natural geochemical process from those caused by applying deicing salt and other human activities. For this more research on the soil characteristics is needed. Continuing the monitoring is necessary in order to better understand the geochemical process and effect of deicing salt on ecosystems in the Bavarian Forest NP. Also comparing our data with that obtained by monitoring at other locations will increase our knowledge, result in a better understanding of trends and result in the better protection of national park ecosystems.

Acknowledgements

REFERENCES

Anonymous (2012) STATISTICA, v. 12, StatSoft, Inc, Tulsa, OK, USA; Available from: http://www.statsoft.com.

Amrhein C, Strong JE, Mosher PA (1992) Effect of deicing salts on metal and organic matter mobilization in roadside soils. Environ Sci Technol 26: 703–709.

Angold P G (1997) The impact of a road upon adjacent heathland vegetation: effects on plant species composition. J App Ecol 34: 409–417.

Bäckström M, Karlsson S, Bäckman L, Folkeson L, Lind B (2004) Mobilisation of heavy metals by deicing salts in a roadside environment. Water Res 38: 720–732.

Bässler C (2004) Das Klima im Nationalpark Bayerischer Wald – Darstellung, Entwicklung und Auswirkung. Nationalparkverwaltung Bayerischer Wald.

Bässler C, Förster B, Moning Ch, Müller J (2009) The BIOKLIM Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest – The conceptual framework, Waldökologie, Landschaftsforschung und Naturschutz, Heft 7: 21–34.

Bryson GM, Barker AV (2002) Sodium accumulation in soils and plants along Massachusetts roadsides. Commun Soil Sci Plant Anal 33: 67–78.

Cunningham MA, Snyder E, Yonkin D, Ross M, Elsen T (2007) Accumulation of deicing salts in soils in an urban environment. Urban Ecosys 11: 17–31.

Czerniawska-Kusza I, Kusza G, Duzynski M (2004) Effect of deicing salts on urban soils and health status of roadside trees in the Opole region. Environ Toxicol 19: 296–301.

Denoel M et al (2010) Cumulative effects of road deicing salt on amphibian behavior. Aquat Toxicol 99: 275–280.

Elling W, Bauer E, Klemm G, Koch H (1987) Klima und Böden. Nationalparkverwaltung Bayerischer Wald.

eMaynadier PG, Hunter ML Jr. (1995) The relationship between forest management and amphibian ecology: a review of the North American literature. Environ Rev 3: 230–261.

Fennessey TW (1989) Guidelines for handling acid-producing materials on low volume roads. Transp Res Rec 1291: 186–189.

Findlay SEG, Kelly VR (2011) Emerging indirect and long-term road salt effects on ecosystems. Ann NY Acad Sci 1223: 58–68.

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29: 207–231.

Gilson MP, Malivia JF, Chareneau RJ (1994) Highway runoff studied. Water Environ Technol 6: 37–38.

Godwin KS, Hafner MF, Buff (2003) Long-term trends in sodium and chloride in the Mohawk River, New York: the effect of fifty years of road-salt application. Environ Pollut 124: 273–281.

Hofstra G, Hall R (1971) Injury on roadside trees: leaf injury on pine and white cedar in relation to foliar levels of sodium chloride. Can J Bot 49: 613–622.

Karraker NE, James PG, James RV (2008) Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecol Appl 18: 724–734.

Křenová Z (2011) Effects of deicing salts in Bavarian Forest National Park, Part I and II. Project report. Ms. Depon in Bavarian Forest NP Authority.

Křenová Z, Chocholoušková Z, Zýval V (2012) Effects of applying deicing salt to roads in protected areas: a preliminary study in the Bavarian Forest National Park. Eur J Environ Sci 2: 56–61.

Mason CF, Norton SA, Fernandez IJ, Katz LE (1999) Deconstruction of the chemical effects of road salt on stream water chemistry. Environ Qual 28: 82–91.

National Research Council (1991) Highway Deicing: Comparing Salt and Calcium Magnesium Acetate. Spec. Rep. 235, Transp. Res. Board,Washington, DC.

Noack EM (1979) Witterung und Klima im Bayerischen Wald. Nationalparkverwaltung Bayerischer Wald.

Ostendorf DW, Pollack SJ, DeCheke ME (1993) Aerobic degradation of CMA in roadside soils: field simulations from soil microcosms. J Environ Qual 22: 299–304.

Richburg JA, Patterson WA, Lowenstein F (2001) Effects of road salt and *Phragmites australis* invasion on the vegetation of a Western Massachusetts calcareous lake-basin fen. Wetlands 21: 247–255.

Rusek J, Rusek J (1999) Impact of winter road salting on soil Collembola and other microarthropods. The conference report: Soil Zoology in Central Europe, České Budějovice.

Trombulack SC, Frissell CA (1999) Review of ecological effects of road on terrestrial and aquatic communities. Cons Biol 14: 18–30.

van der Ree R, Smith DJ, Grilo C (2015) Handbook of the road ecology. Wiley Blackwell.

Wrobel M, Tomaszewicz T, Chudecka J (2006) Floristic diversity and spatial distribution of roadside halophytes along forest and field roads in Szczecin lowland (West Poland). Polish J Ecol 54: 303–309.

Yousef YA, Wanielista MP, Harper HH (1985) Removal of highway contaminants by roadside swales. Transp Res Rec 1017: 62–68.

Zýval V, Křenová Z, Chocholoušková Z, Zýval V Jr., Zývalová J (2015) Effects of applying deicing salt to roads in protected areas of the Bohemian Forest region. Silva Gabreta 21: 43–52.

Zýval V, Křenová Z, Raus M, Štrupl V, Zýval V Jr., Zývalová J (2018) Effects of Deicing Salt in Protected Areas: Water Quality Monitoring in the River Basin with the Occurrence of a Rare Pearl Mussel. J Polish Mineral Eng Soc January–June: 99–102.

WIND CHARACTERISTICS RECORDED AT THE CZECH CARBON OBSERVATION SYSTEM (CZECOS) SITE RAJEC

SHILPI CHAWLA[1,2,*], VINH XUAN NGUYEN[1,2,3],
CARLOS P. GUERRA TORRES[1,2,4], MARIAN PAVELKA[1],
JAN TRUSINA[1], and MICHAL V. MAREK[1]

[1] Global Change Research Institute CAS, Bělidla 986/4a, 603 00 Brno, Czech Republic
[2] Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 1, 613 00 Brno, Czech Republic
[3] Department of Ecology, Institute of Tropical Biology VAST, 85 Tran Quoc Toan Street, District 3, Ho Chi Minh City, Vietnam
[4] Department of Botany, University of Panama P.O. 0824-00077 Panama, Panama
* Corresponding author: chawla.s@czechglobe.cz

ABSTRACT

The main aim of this study is to investigate general and temporal characteristics of wind speed and direction at Rajec Ecosystem Station (ES), which is part of the Czech Carbon Observation System (CzeCOS) network and located in the Czech-Moravian highlands in the Czech Republic. Four years (2013–2016) of eddy covariance data recorded in a mature monoculture of spruce (Picea abies) was used to build wind roses and analyse the temporal wind characteristics. The prevailing wind directions at Rajec ES were South-East and North-West and the highland orography in this region does not affect wind flow. Changes in wind direction were recorded each year mainly due to changes in the general atmospheric circulation patterns over Europe. This paper records the occurrence of calm conditions and a threshold of horizontal wind speed (u) of less than 1 m s^{-1}, was used to define calm periods. The average percentage of calm conditions over 4 years was 6% and when the data was separated into daytime and nighttime occurrence of calm conditions, it was 8% and 4%, respectively.

Keywords: calm conditions; eddy covariance; wind characteristics; wind rose

Introduction

The eddy covariance (EC) method is a common method used to determine the exchange of energy and matter between a surface and the atmosphere. It is the most direct and accurate approach for investigating turbulent exchange of water vapour and trace components between an ecosystem and the atmosphere (Burba 2013). The EC method determines gas transport by turbulent eddies in real time, which enables one to calculate turbulent fluxes within the atmospheric boundary layer.

It is important to note that changes in the pattern and speed of wind can influence the measurement of fluxes using the EC method. Calm or low wind conditions affect the accuracy of the measurement using an EC system, as the fluxes are often biased under low-wind conditions due to low turbulence (Burba 2013). Wind analysis can help in identifying these problematic periods of low wind intensity. Another application of this type of study can be for silviculture, as practices like thinning of stands result in wind tunnelling and affects the sustainability of forest stands (Mayhead et al. 1975; Cremer et al. 1982; Gardiner et al. 1997). Major thinning in forests increases the roughness of the canopy surface (Cremer et al. 1982), which poses a threat to the trees during gales. Knowledge of the prevailing wind direction in a region can help in planning silviculture treatments in a way that damage of forest stands due to channelling of high winds can be prevented. This will increase the stability of forests and protect them from damage by wind.

The aim of the current study is to investigate the pattern of wind at Rajec Ecosystem Station (ES) and describe the attributes of wind in different seasons/periods of calm (u < 1 m s^{-1}) and dynamical (u > 1 m s^{-1}) wind conditions over the years 2013–16.

Material and Methods

Site Description

The Rajec ES near the town Rajec-Jestrebi is situated in the Czech-Moravian highlands in the Czech Republic. The coordinates of the ES are 49°26′37″N, 16°41′47″E and the altitude is 610–625 m a.s.l. The mean annual temperature over the last few decades (1975–2012) is 7.5 ± 1.2 °C and the mean annual precipitation 673 ± 144 mm. The ES is situated in a mature, currently 117 year old forest consisting of a monoculture of spruce (*Picea abies*). The height of this stand was 33 m in 2013 (Markova et al. 2017).

The collection of EC data at Rajec ES started in the year 2012. This ES is part of the national network CzeCOS (Czech Carbon Observation System), the international network ICOS (Integrated Carbon Observation System), national complement of significant infrastructures within ESFRI (European Strategy Forum on Research Infrastructures) and the site is a long-term research station LTER (Long Term Ecological Research).

Instrumentation

The EC system at Rajec ES is equipped with a 3D sonic anemometer (Gill R3 by Gill Instruments, UK), which

was used for measuring wind speed and direction and was placed 41 m above the ground surface which was approximately 8 m above the surface of the canopy.

Data

This study uses 4 years of data (2013–2016); Microsoft Excel was used for the analysis. Wind data from the EC system was sampled at 20 Hz and time-averaged over 30 minute periods. A threshold of horizontal wind speed (u) less than 1 m s^{-1}, was used to define calm periods when turbulence was low (Burba 2013).

The four year data set was quality checked, which revealed some gaps in the data. The percentage of missing data was 6.32% in 2013, 7.77% in 2014, 7.05% in 2015 and 0.11% in 2016. The horizontal wind speed data were binned in eight direction classes (Table 1). The percentage of calm conditions (u < 1 m s^{-1}) was determined separately for daytime (06:00–18:00), night-time (18:00–06:00), per month and per season. The seasonal characteristics of wind were evaluated for four seasons separately, winter (December–February), spring (March–May), summer (June–August), autumn (September–November). The data was also evaluated for non-growing and growing periods of the year, November–April and May–October respectively. Hajkova et al. (2012) describe May-October as the main growing season of plants in temperate areas in the northern hemisphere.

Table 1 Wind direction classes and their corresponding degree values.

Direction	Degree
North (N)	0–23 and 338–360
North-East (NE)	23–68
East (E)	68–113
South-East (SE)	113–158
South (S)	158–203
South-West (SW)	203–248
West (W)	248–293
North-West (NW)	293–338

Results and Discussion

The prevailing wind directions at Rajec ES was northwest (NW) and south-east (SE) over the whole year (Figs. 1 and 2). Four years data revealed that the wind direction on average was 18% SE, 17% NW, 13% N and 10% S. This is in accordance with general wind pattern in the Czech-Moravian Highlands, which commonly have NW and SE wind directions (Tolasz et al. 2007).

Seasonal variations in wind direction were recorded (Fig. 3). Tolasz et al. (2007) report that central Europe is mainly influenced by westerly winds and the Czech Republic is among the areas that have dominant effects of the Azores pressure high, Icelandic depression and Siberian high, which effects the wind characteristics during different periods of the year. The observations at ES Rajec

show that wind during winter predominantly came from the SW and NE, and shifted direction during spring and summer to NW, N and NE. However, during autumn, SE, N and NW were the prevailing wind directions. This can be explained by the general atmospheric circulation patterns over central Europe and potentially by the local circulation, which is modified by the terrain. Border-mountains, individual mountain saddles, valleys and orientation of slopes are some factors that can affect the direction of wind (Tolasz et al. 2007). A similar study to the current one was done by Havránková and Sedlák (2004) for another CzeCOS-ICOS ecosystem station, Bily Kriz, in the Beskydy Mountains in the Czech Republic and it also highlights a strong connection between wind patterns and local topography.

However, a comparison of the results of the current study at ES with those of surrounding meteorological stations at Kucharovice, Svratouch and Brno, operated by the Czech Hydrometeorological Institute (Tolasz et al. 2007), revealed similar wind conditions for all these sites. The other meteorological stations are situated in open terrain well away from significant effects from surrounding barriers. Thus, topography in the surroundings of Rajec ES apparently have only a negligible modifying effect on the wind patterns at ES and therefore we assume that the variations in wind direction during a year are predominantly caused by changes in the regional atmospheric circulation patterns.

For the wind speed analysis, we used different wind speed classes starting from 0–1 m s^{-1} to greater than 12 m s^{-1}. At Rajec ES calm wind conditions (< 1 m s^{-1}) were not very common (Table 2). The percentage of calm wind conditions over a whole year was 5.4, 5.6, 5.8 and 6.7% for 2013, 2014, 2015 and 2016, respectively. The occurrence of calm conditions at nearby stations (Kucharovice, Svratouch, Brno) was also not very high and similar to that recorded at Rajec ES. It is worth noting that strong winds stronger than 10 m s^{-1} were also not frequent at Rajec ES and occurred more frequently in winter than summer. Thus, this study confirmed that wind speed in most parts of the year is in the range of 1–3 m s^{-1} (Fig. 4).
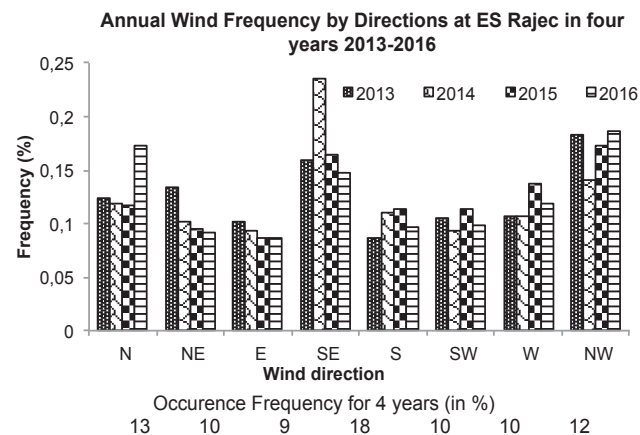
Fig. 1 Annual relative wind frequency by direction recorded each year at the Rajec ecosystem station (2013–16).

**Table 2** Percentage of calm wind conditions (u < 1 m s⁻¹) during different periods of a year.

(All values are percentages of the time during a particular period)					
Year	2013	2014	2015	2016	Average
Whole year	**5%**	**6%**	**6%**	**7%**	**6%**
Daytime	7%	8%	8%	9%	8%
Night-time	4%	3%	4%	5%	4%
May–Oct (growing season)	**5%**	**7%**	**6%**	**6%**	**6%**
% of day-time	7%	10%	8%	8%	8%
% of night-time	2%	4%	5%	3%	4%
Nov–Apr (non-growing season)	**6%**	**4%**	**5%**	**7%**	**6%**
% of daytime	7%	6%	8%	9%	7%
% of night-time	5%	3%	3%	6%	4%

The percentage of calm conditions in the growing and non-growing season during 2013–16 was 6% and when the data was analysed separately for day- and night-time, calmer conditions were recorded during day-time (Table 2). The reason for this is the subject of a further investigation.

Conclusions

The prevailing wind direction over the course of a year at Rajec ES was SE and NW. Seasonal shifts in the prevailing wind directions were recorded in all four years. During winter, the wind came predominantly from the SW and NE and shifted during spring and summer to NW, N, NE. Main wind directions during autumn were SE, N, NW.
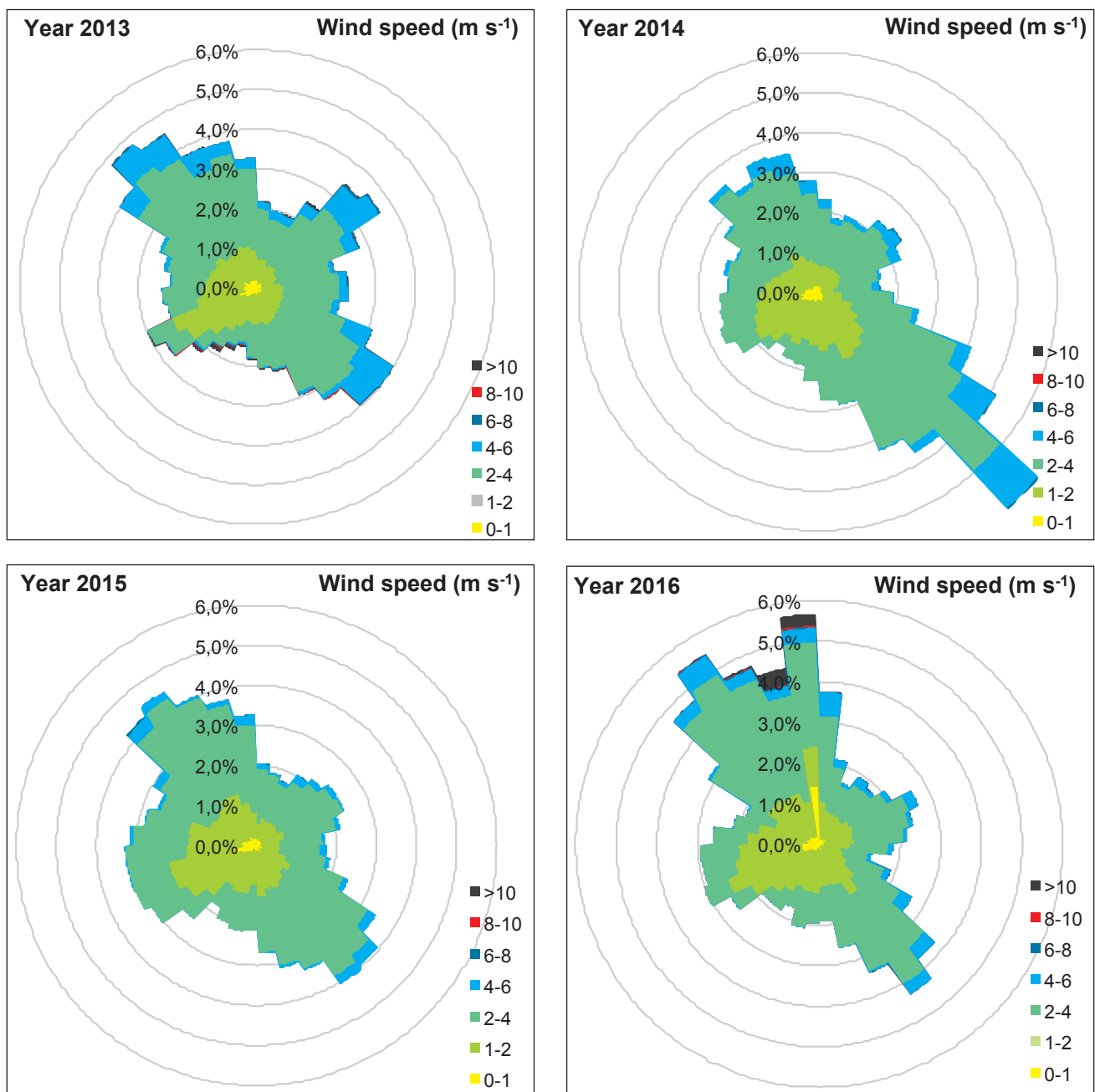
Fig. 2 Annual wind roses recorded at the Rajec ecosystem station (2013–16).
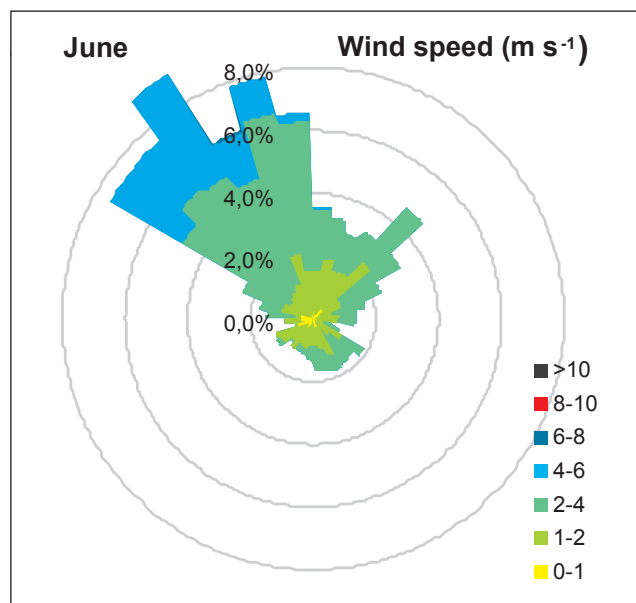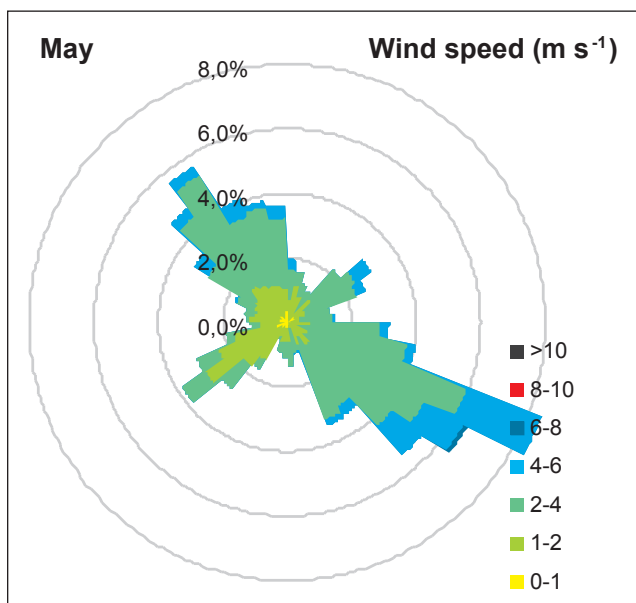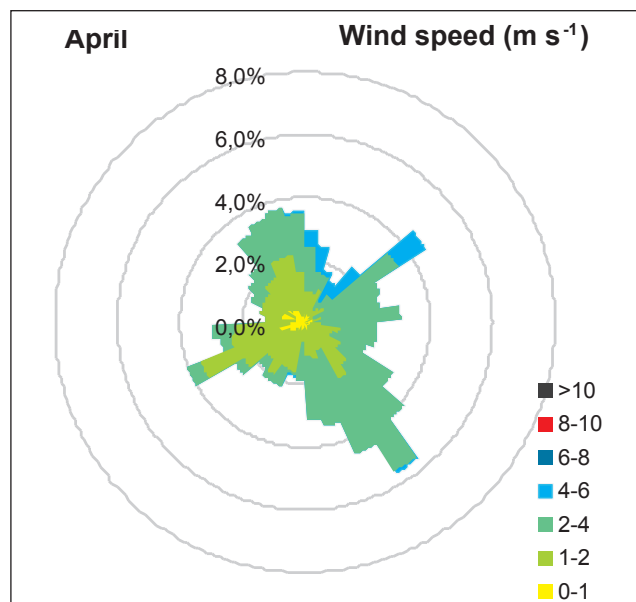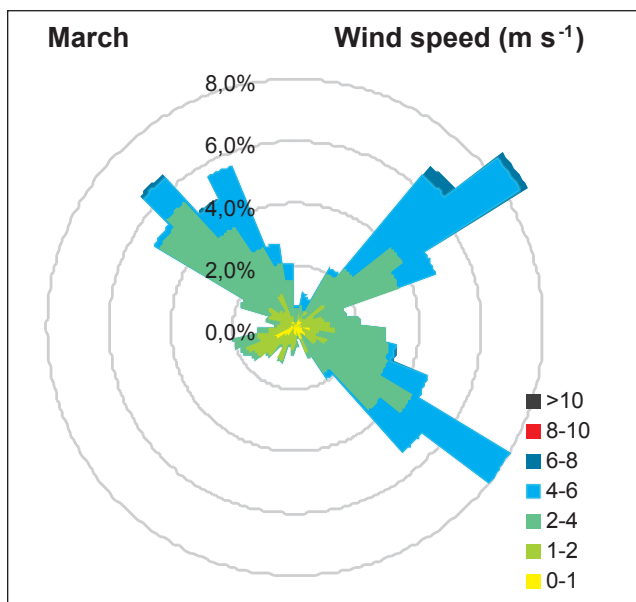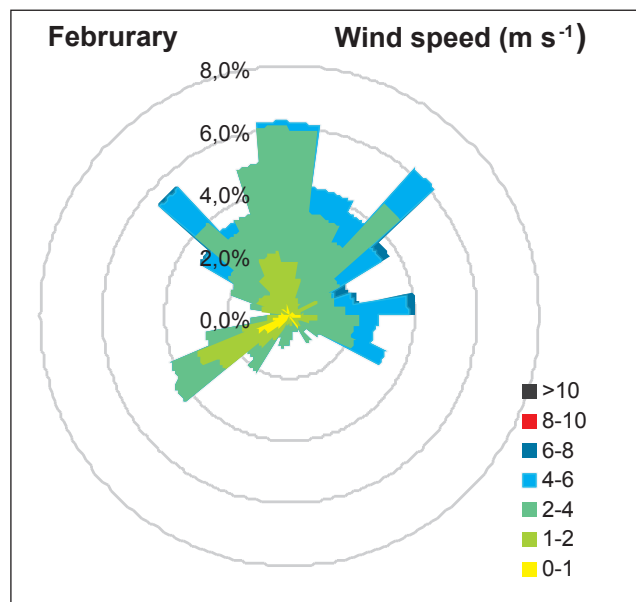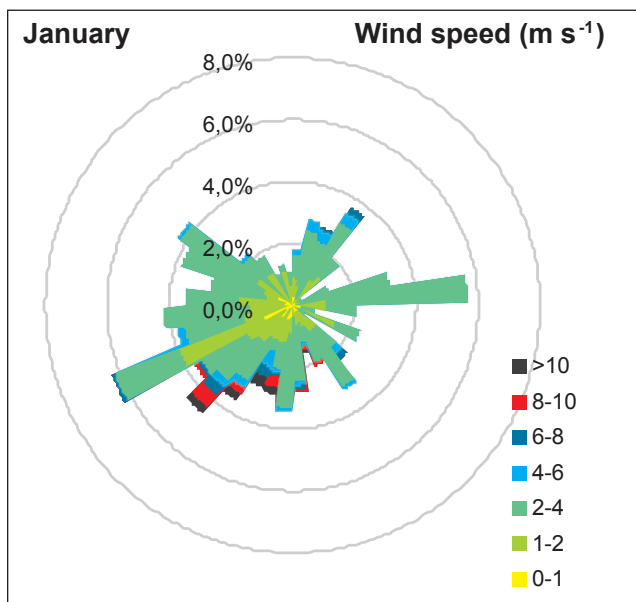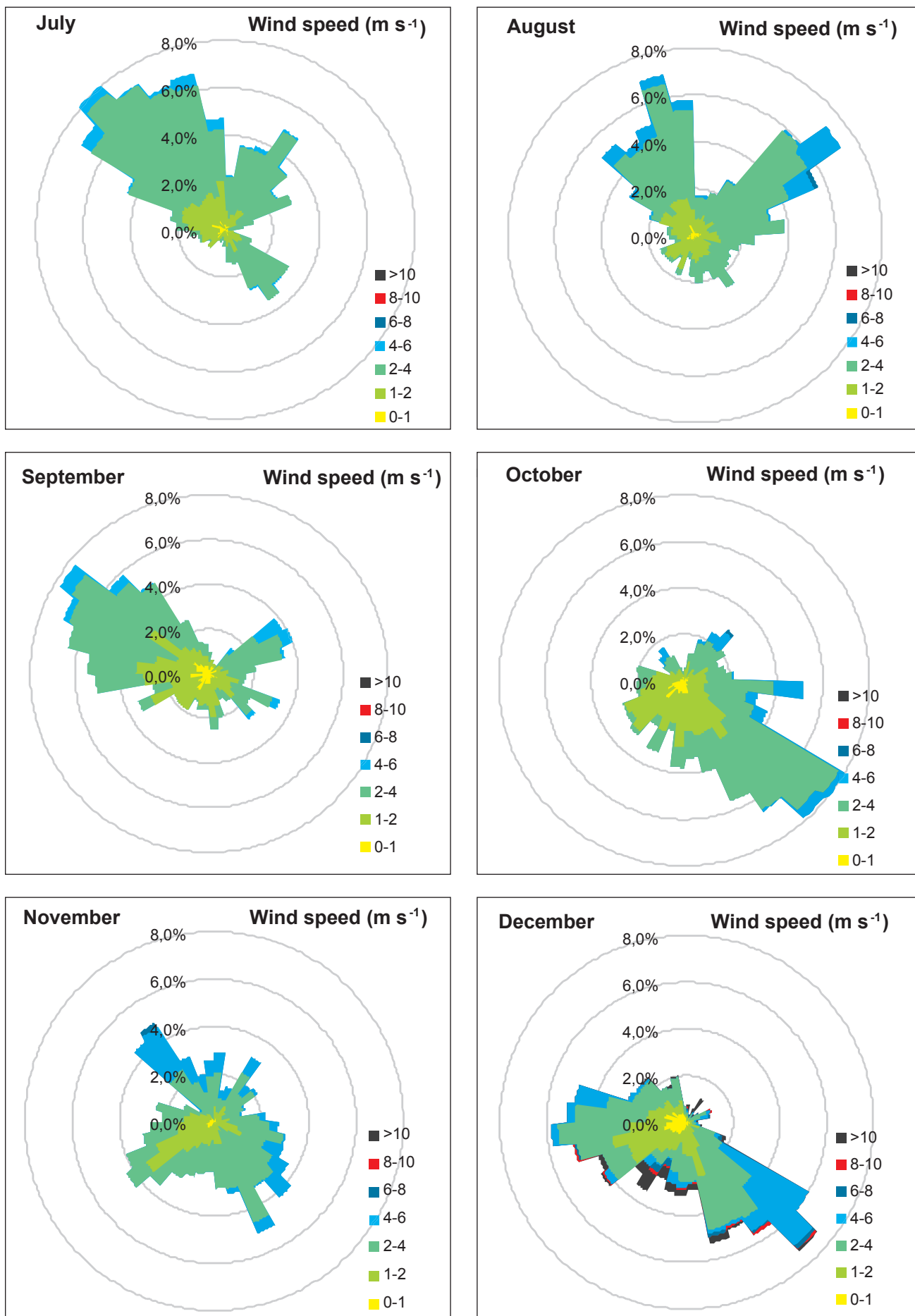
Fig. 3 Monthly wind roses recorded at Rajec ecosystem station during the year 2013**.**
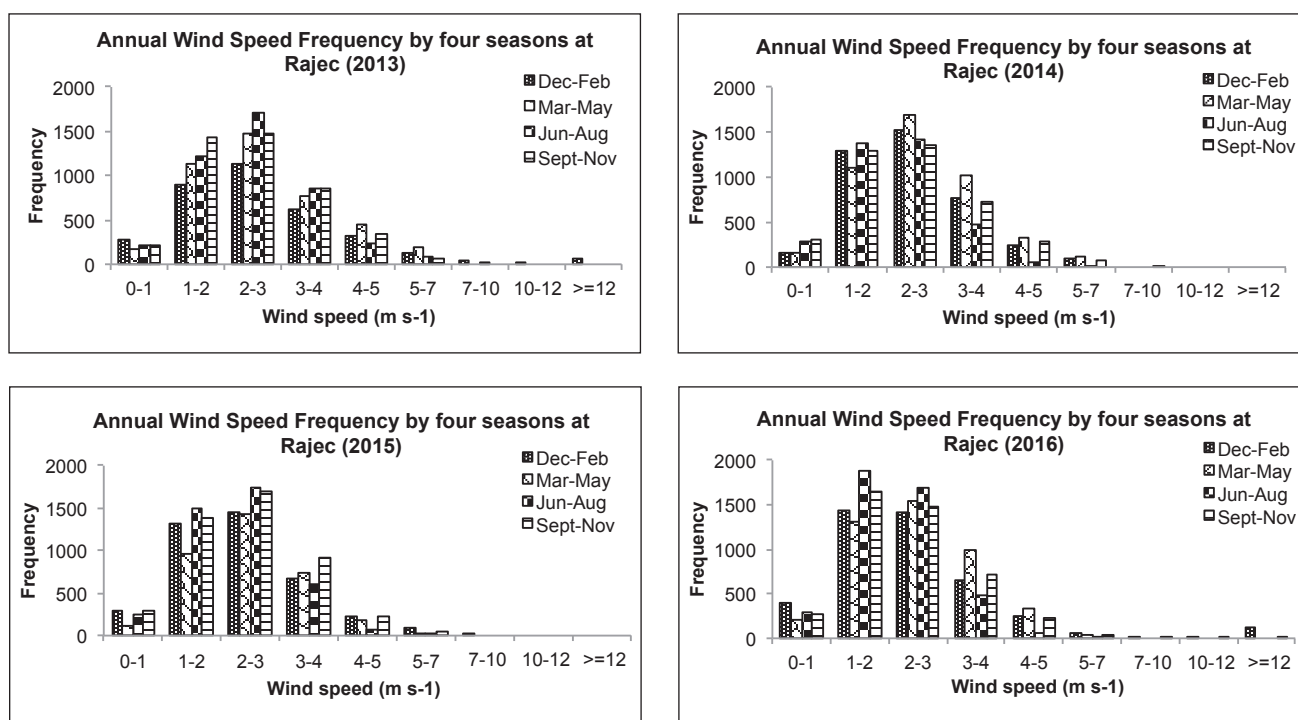
Fig. 4 Annual Wind Speed Frequency recorded in four seasons at the Rajec ecosystem station.

The wind analysis at Rajec corresponds well with those of nearby stations (Kucharovice, Svratouch, Brno). Since the nearby World Meteorological Organization (WMO) stations are open terrain stations with a minimum influence of local topography on wind patterns, we can conclude that the local orography at ES Rajec has very little influence on the wind patterns recorded there. The shift in wind direction during the year at Rajec is determined more by changes in the general circulation patterns over the seasons.

The analysis of the winds recorded at Rajec ES indicates that there are only short periods with strong winds (>10 m s^{-1}) that pose a threat to the forests in this area. Over the long term, climate change scenarios indicate an increase in extreme weather phenomena; therefore, management practices like thinning and restoration of forest need to consider the prevailing wind directions in order to increase the sustainability of the forest.

The percentage of periods with calm wind conditions (threshold value of u < 1 m s^{-1}) at Rajec ES is relatively low, an average of 6% for all the years included in this study. The most common range in wind speed per year is 1–3 m s^{-1}, followed by 4–5 m s^{-1}. Wind speeds above 10 m s^{-1} are not usual at Rajec ES. The observed wind conditions at Rajec ES favour the application of the EC method. These wind conditions generally result in a good mixing of the air masses across the forest canopy, which may account for the high quality the EC data and considerable reduction in the potential bias in the derived fluxes. The knowledge of low wind conditions and frequency of their occurrence help to identify problematic periods for EC measurements, which may arise due to low atmospheric turbulence.

On average over the course of the four years of this study, calmer conditions were more frequently recorded during daytime than night-time, which contrasts with most of the eddy covariance study observations at other sites (Burba 2013). The evaluation of the reasons for this observation is beyond the scope of the current study.

Acknowledgements

REFERENCES

Burba G (2013) Eddy Covariance Method for scientific, industrial, agricultural and regulatory applications A Field Book on Measuring Ecosystem Gas Exchange and Areal Emission Rates LI-COR Biosciences, Lincoln, NE, USA.

Cremer KW, Borough CJ (1982) Effects of stocking and thinking on wind damage in plantation. NZ J Forestry Sci 12: 244–68.

Gardiner BA, Stacey GR, Belcher RE, Wood CJ (1997) Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. Forestry 70: 233–52.

Hajkova L, Vozenilek V, Tolasz R, Kohut M, Mozny M, Nekovar J, Novak M, Richterova D, Striz M, Vavra A, Vondrakova A (2012) Atlas of the phenological conditions in Czechia. Cesky Hydrometeorologicky Ustav. Olomouc, Czech Republic.

Havrankova K, Sedlak P (2004) Wind velocity analysis for mountainous site Bily Kriz. Ecologia (Bratislava) 23: 46–54.

Mayhead GJ, Gardiner JB, Durrant DW (1975) A report on the physical properties of conifers in relation to plantation stability.

UK Forestry Commission, Research and Development Division Report.

Markova I, Pavelka M, Taufarova K, Krejza J, Janous D (2017) Meteorological Yearbook 2013. Centrum Vyzkumu Globalni Zmeny AV CR, v.v.i., 2017, pp 124.

Tolasz R, Brazdil R, Bulir O, Dobrovolny P, Dubrovsky M, Hajkova L, Halasova O, Hostynek J, Janouch M, Kohut M, Krska K, Krivancova S, Kevton V, Lepka Z, Lipina P, Mackova J, Metelka L, Mikova T, Mrkvica Z, Mozny M, Nekovar J, Nemec L, Pokorny J, Reitschlager JD, Richterova D, Roznovsky J, Repka M, Semeradova D, Sosna V, Striz M, Sercl P, Skachova H, Stepanek P, Stepankova P, Trnka M, Valerianova A, Valter J, Vanicek K, Vavruska F, Vozenilek V, Vrablik T, Vysoudil M, Zaruba J, Zuskova I (2007) Atlas Podnebí Česka (Climate atlas of Czechia). Czech Hydrometeorological Institute, Palacky University, Olomouc.

IS MEASURING OF TEMPERATURE FLUCTUATIONS FOLLOWING BARK BEETLE INFESTATION IN DIFFERENTIALLY MANAGED FORESTS OBJECTIVE?

KAROLÍNA BÍLÁ*

Department of Biodiversity Research, Global Change Research Institute CAS, Bělidla 986/4a, 60300 Brno, Czech Republic
* Corresponding author: kcerna@volny.cz

ABSTRACT

Proper management of woods infested by bark beetle – clearing infested trees to prevent spread of bark beetle, or leaving them to preserve biodiversity – is a hotly debated topic. Differences in temperature regime between differentially managed areas are often-used arguments in these discussions. Results from the field measurements are confusing. Therefore, here we review previous studies and report our results of using thermal sensors in the field to determine the factors that might affect the differences in temperature reported in previous papers. Our results indicate that the variability recorded in one particular habitat, dry forest, is associated with the specific characteristics of the locality of each microsite/sensor. We conclude that it is important to consider not only the temperatures recorded but also describe microsites in detail in terms of vegetation structure, sunshine or numbers of trees per unit area.

Keywords: bark beetle; climate change; forest management; iButton; temperature; thermal sensor

Introduction

Recent discussions about the effect the predicted changes in climate will have on the Šumava National Park (NP) reveal a difference in opinions on how best to manage forests attacked by bark beetles in order to preserve natural conditions and the biodiversity in this valuable area. The first opinion recommends clear felling infested forest in order to stop the bark beetles spreading further (Wermelinger 2004; Zahradník 2004), the second prefers no human interference with natural processes and leaving the dead trees standing (Jonášová and Prach 2004; Hais et al. 2009).

One of the main arguments is that the microclimate in forest differently managed after bark beetle attack differs. Clear felling of infested trees might reduce the number of bark beetles; however, it can also negatively affect the temperature and water regime at such sites (Kindlmann et al. 2012; Bílá 2016). What happens if dead trees are left standing at infested sites and no management is applied?

Several studies report differences in microclimate in cleared (Fig. 1) compared to dead (Fig. 2) and green forests (Tesař et al. 2004; Hais and Kučera 2008; Šantrůčková et al. 2010; Kindlmann et al. 2012; Hojdová et al. 2015; Matějka et al. 2016) but the results are inconsistent. Some authors claim that the climate in a dead forest is more similar to that in a green healthy forest (Šantrůčková et al. 2010; Kindlmann et al. 2012; Matějka et al. 2016). Others claim that it is more similar to that in a clear felled area of forest (Hais and Pokorný 2004; Tesař et al. 2004; Hojdová et al. 2015). Which is closer to the truth? This review attempts to resolve such contrary statements and elucidate microclimate changes, particularly in temperature, in the Šumava NP.

Methods

Published papers dealing with temperature changes in the Šumava NP are based either on data loggers/thermal sensors or on a combination of remote sensing with GIS layers. These measurements usually compare microclimate conditions in green mature forest, dead dry forest and clearings in order to propose the best type of management to preserve natural forest habitats in the Šumava Mts.

Remote sensing/GIS

Studies based on data from remote sensing record significant warming in areas of forest attacked and killed by bark beetles. Hais and Kučera (2008) present changes in land cover and associated changes in temperature ranging from the coldest to the warmest associated with the decay of mountain spruce forests. They measured a mean temperature increase of 5.2 °C in the clear-felled areas and of 3.5 °C in spruce forest killed by bark beetles (examples of these habitats are presented in Figs. 1 and 2). However, forest areas of conservation interest are located at higher altitudes and this might be important in determining the difference when using remote sensing (Barry 1992).

Data loggers/thermal sensors

Measuring temperatures with thermal sensors is more accurate in terms of focusing on specific localities. Sensors are usually placed below the ground, on the surface, above the herbaceous layer or in the air (Fig. 3). The advantage of thermal sensors is that they record temperatures continuously in adjusted time sequences. Their placement determines the level of radiation from the sun they are exposed to (sensors can be placed underground or in vegetation or exposed to direct sunlight) and con-
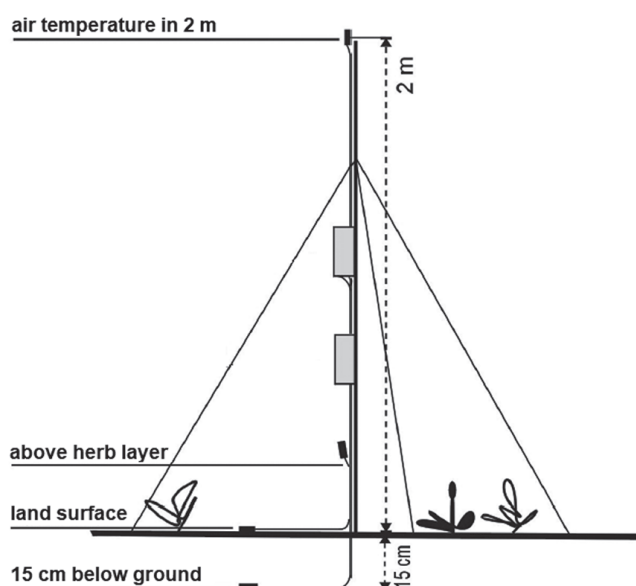
Fig. 1 Aerial photograph of a clear felled area of forest in the Šumava NP (author: Zdenka Křenová).

Fig. 2 Aerial photograph of a dead forest area that resulted from a bark beetle attack being naturally recolonized by young trees of *Picea abies* in the Šumava NP (author: Zdenka Křenová).

Fig. 3 Thermal sensors placed at different heights: 15 cm below the ground, on the surface, above the herbaceous plant layer and 2 m above the surface of the ground.

Fig. 4 Thermochron/iButton (model DS1921G) – a practical and inexpensive data logger of small size.

sequently the values recorded differ accordingly. We assume that differences in the degree of exposure of sensors to sunlight is one of the reasons why the published results differ.

Thermal sensors were used by several authors and one group recorded very similar temperature conditions in dead forest and green healthy forest, whereas other scientists recorded similar temperatures in dead forest and clearings. All authors agree on that temperature fluctuations are lowest in green living forest. Šantrůčková et al. (2010) report the peak day and night temperatures recorded during August in the vicinity of Březník in the Šumava NP. In dead and green forest, they fluctuated very similarly, between 5–10 °C and in clearings the fluctuations were greater than 30 °C. Slightly higher temperatures were recorded in the dead forest (Kindlmann et al. 2012), namely the maximum air temperature recorded at a height of 2 m: in green forest it was 21.6 °C, in dry forest 34.6 °C and in clearing 39.7 °C. These results confirm those of Hais and Kučera (2008) that temperatures and daily amplitudes are greater in dead spruce forests than in green forests; however, temperatures in clearings are even higher than in dead spruce forests. Pokorný (2011) mentions an increase in the maximum temperatures in dry forest of almost about 20 °C, which is the same as in clearings.

Hojdová et al. (2005) present similar results with the maximum daily temperature amplitude above herbaceous plants in dead forest on average 14.5 °C and in clearings 16.7 °C during the vegetative season in 2002 and 2003. Moreover, Tesař et al. (2004) suggest the living and transpiring vegetation has a cooling effect and that the most extreme thermal environment is recorded in dead forest (daily maximum temperature measured: dead forest above 30 °C, 23–25 °C and living forest 22 °C).

We conducted a small experiment with thermochrons/iButtons (model DS1921G, Fig. 4) and exposed five thermochrons in dry forest killed by bark beetles > 10 years previously. We attempted to select microsites with different types of vegetation cover and exposure to different levels of sunshine (Table 1). Temperatures were measured every hour.

The main goal of this small experiment was to reveal that there could be large differences in temperatures recorded even within one type of habitat (dry forest attacked and killed by bark beetles more than 10 years previously). Variability in the recordings of the 5 iButtons is presented in Figs. 5 and 6, in which temperature fluctuations (i.e. maximum – minimum daily temperatures) and maximum daily temperatures are displayed. There is an obvious effect of the structure of the vegetation, with shading important in reducing the exposure to direct sun light.

Discussion

Temperature regime in the Šumava NP has recently been widely discussed among politicians and scientists. There is evidence that increased temperatures promote bark beetles to attack larger areas of forest and cause devastating damage. Bečka and Beudert (2016) report a summer air temperature increase of about 2 °C since 1978. In particular, droughts and increases in temperature are favourable conditions for bark beetle attacks, which occur more frequently and are more serious under these conditions (Hais and Kučera 2008; Kindlmann et al. 2012). Bark beetles benefit from higher temperatures as they are able to raise two rather than one generation per year at high altitudes (Økland et al. 2015). Therefore,

| iButton code	Description	Photo
C2	VEGETATION COVER: 25% *Picea abies* – alive 25% *Picea abies* – dead 30% *Vaccinium myrtillus* 20% *Calamagrostis villosa* SUN EXPOSURE: 30% shadow 70% sunlight	
C3	VEGETATION COVER: 10% *Picea abies* – alive 50% *Picea abies* – dead 15% *Vaccinium myrtillus* 35% *Calamagrostis villosa* SUN EXPOSURE: 70% shadow 30% sunlight	
C4	VEGETATION COVER: 15% *Picea abies* – alive 10% *Picea abies* – dead 40% *Vaccinium myrtillus* 30% *Calamagrostis villosa* 5% *Avenella flexuosa* SUN EXPOSURE: 80% shadow 20% sunlight	

| C5 | VEGETATION COVER:
20% *Picea abies* – alive
20% *Picea abies* – dead
5% *Vaccinium myrtillus*
25% *Calamagrostis villosa*
30% *Avenella flexuosa*

SUN EXPOSURE:
50% shadow
50% sunlight | |
| C6 | VEGETATION COVER:
25% *Picea abies* – alive
30% *Picea abies* – dead
5% *Vaccinium myrtillus*
10% *Avenella flexuosa*
30% moss layer

SUN EXPOSURE:
30% shadow
70% sunlight | |

Table 1 Five microsites with different vegetation cover and exposure to sun in dry unmanaged forest. Red circles indicate position of the iButton.

there are long debates about the proper management of infested woods. One proposal is to fell and remove every infested tree, while others want to leave dead trees standing and in so doing help the regeneration of understory vegetation.

One of the arguments is that changes in microclimate occur in dry dead forest and clearings. Here, we compare several studies with very different results and we would like to elucidate why the measurements differ. After a short field-test with iButtons we suppose that one of the most important factors is the microclimate in which thermal sensor is placed. That is, vegetation cover and shadow/sunshine must be taken into account. In dry forest, the shading from standing dead stems and density of these stems is another factor that needs to be considered. Furthermore, forest regeneration was observed at sites after bark beetle attack, i.e. in standing dry forest.

Clearings can affect a site so that natural forest regrowth will not be possible. Cut trees and wood transport from the site changes the biotic and abiotic conditions at a site. The moss layer might disappear and competitive species of grass (*Calamagrostis villosa*, *Avenella flexuosa*) dominate the herbaceous plant layer (Kučerová et al. 2008). Several studies mention that large gaps in forests (more than 15 m in diameter) host much lower seedlings densities and present a more competitive environment for understory vegetation (Grenfell et al. 2011; Downey et al 2018). In contrast, smaller gaps in forests caused by disturbances provide space for new species and promote biodiversity. Forest gaps or their edges are often recognized as hotspots of insect diversity (Müller et al. 2007; Kautz 2013). Thus, native bark beetles play an important role in forest ecosystems around the world and commonly help promote forest succession (Bentz et al. 2010).
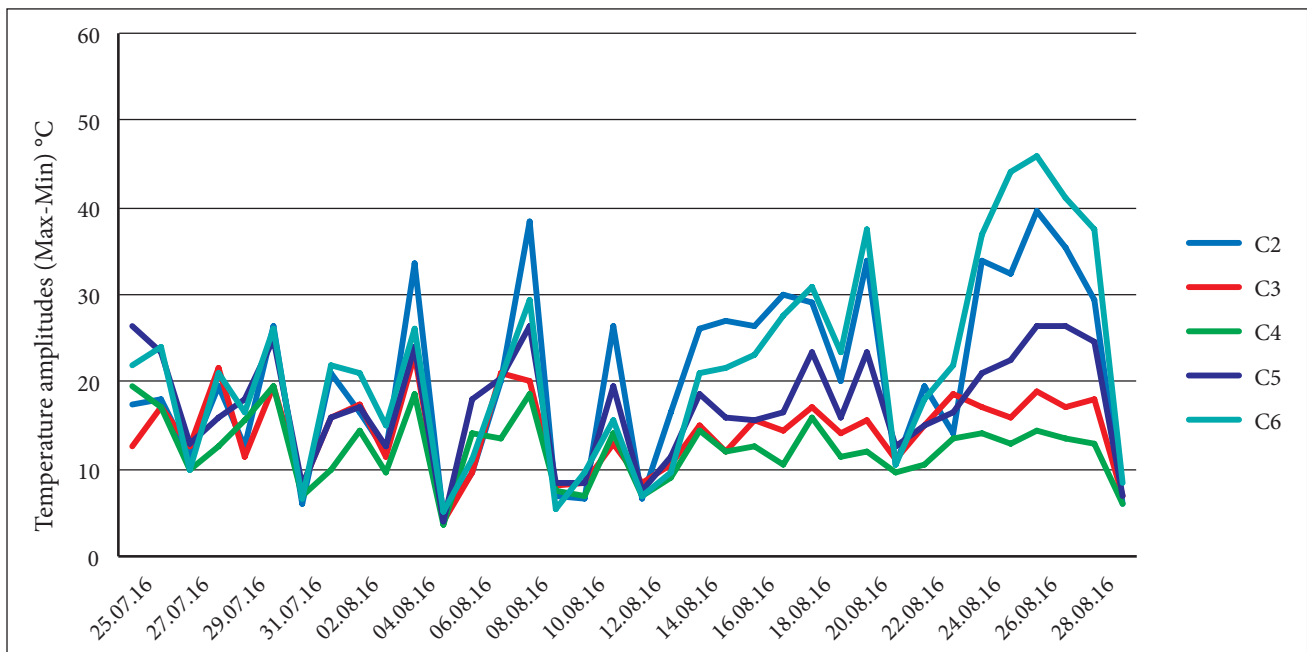
Fig. 5 Differences between the minimum and maximum daily temperatures recorded by iButtons (C2–C6) placed in a dead forest in July and August 2016.
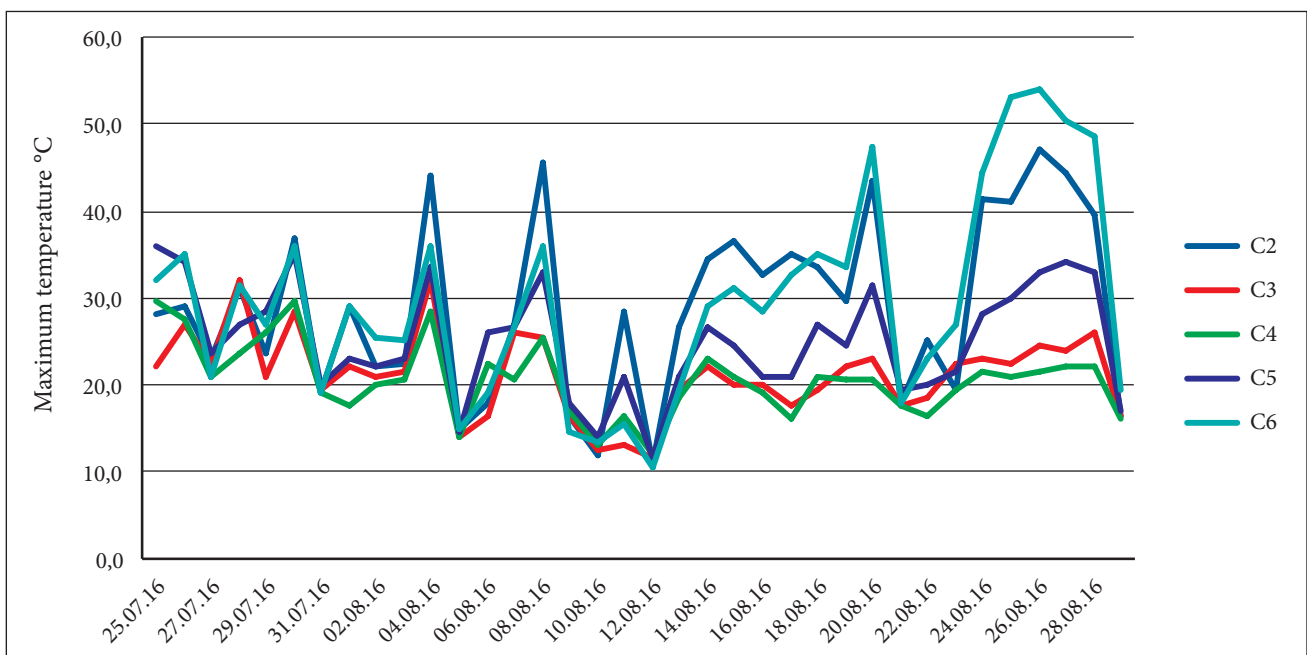
Fig. 6 Maximum daily temperatures recorded by iButtons (C2–C6) in a dead forest in July and August 2016.

In dead forest, herbaceous plants and mosses survived undamaged at our study sites. There is also a positive effect of the shading of undergrowth by dead trees even though these trees no longer transpire. Under dead trees, new forest regenerates fast and without any management or additional costs (Čížková et al. 2011). Cleared areas, on the other hand, are not very favourable for tree seedlings because of changed structure in the vegetation, an open canopy and exposure to direct sunshine, together with changes in the temperature and water regimes (Jonášová and Prach 2004; Schwarz 2013; Bílá 2016). Moreover, artificial planting is expensive and is subject to many risks. Trees are usually all planted at the same

time, which results in a forest in which the trees are all the same age. Such a forest needs permanent care and is liable to natural disturbances and enemies.

Both types of management after a forest is attacked by bark beetle were applied in the Šumava National Park. Differences in forest succession and environmental conditions were recorded recently at these sites. Based on this knowledge, we should not forget that the main aim of national parks is to protect endangered habitats and their biodiversity (Šíp 2004; Nikolov et al. 2014; Kindlmann and Křenová 2016). Disturbances, dying trees, natural regeneration and spontaneous regrowth are common and natural components of national parks.

Acknowledgements

REFERENCES

Barry RG (1992) Mountain weather and climate, 2nd edn. Routledge, London, New York.

Bečka P, Beudert B (2016) Kůrovec a voda. Jak bezzásahovost ovlivňuje vodní režim na Šumavě. Šumava, jaro: 16–17. In Czech.

Bentz BJ, Régnière J, Fettig CJ, et al. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60: 602–13.

Bílá K (2016) Are bark beetles responsible for drouhgts in the Šumava Mts.? Eur J Environ Sci 6: 108–113.

Čížková P, Svoboda M, Křenová Z (2011) Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. Silva Gabreta 17: 19–35.

Downey M, Valkonen S, Heikkinen J (2018) Natural tree regeneration and vegetation dynamics across harvest gaps in Norway spruce dominated forests in southern Finland. Canadian J Forest Res 48: 524–534.

Grenfell R, Aakala T, Kuuluvainen T (2011) Microsite occupancy and the spatial structure of understorey regeneration in three late-successional Norway spruce forests in northern Europe. Silva Fenn 45: 1093–1110.

Hais M, Jonášová M, Langhammer J, Kučera T (2009) Comparison of two types of forest disturbance using multitemporal Landsat TM/ETM+ imagery and field vegetation data. Remote Sens Environ 113: 835–845.

Hais M, Kucera T (2008) Surface temperature change of spruce forest as a result of bark beetle attack: Remote sensing and GIS approach. Eur J Forest Res 127: 327–336.

Hais M, Pokorný J (2004): Changes in land cover temperature and humidity parameters resulting from spruce forests decay. Aktuality šumavského výzkumu II: 49–55.

Hojdová M, Hais M, Pokorný J (2005) Microclimate of a peat bog and of the forest in different states of damage in the National Park Šumava. Silva Gabreta 11: 13–24.

Jonášová M, Prach K (2004) Central-Europen mountain spruce forests: regeneration of tree species after a bark beetle outbreak. Ecol Eng 23: 15–27.

Kautz M, Schopf R, Ohser (2013) The "sun-effect": microclimatic alterations predispose forest edges to bark beetle infestations. Eur J Forest Res 132: 453–465.

Kindlmann P, Křenová Z (2016) Biodiversity: Protect Czech park from development. Nature 531: 448.

Kindlmann P, Matějka K, Doležal P (2012) Lesy Šumavy, lýkožrout a ochrana přírody. Karolinum, Praha. In Czech.

Kučerová A, Rektoris L, Štechová T, Bastl M (2008) Disturbances on a wooded raised bog – How windthrow, bark beetle and fire affect vegetation and soil water quality? Folia Geobotanica 43: 49–67.

Matějka K, Starý J, Boháč J, Lepšová A, Špulák O (2016) Demonstration and research plots for monitoring of forest management in protected areas. https://www.infodatasys.cz/BiodivLes

Müller J, Bussler H, Gossner M, Gruppe A, Jarzabek-Müller A, Preis M, Rettelbach T (2007) Forest edges in the mixed-montane zone of the Bavarian Forest National Park – hot spots of biodiversity. Silva Gabreta 13: 121–148.

Nikolov Ch, Konôpka B, Kajba M, Galko J, Kunca A, Janský L (2014) Post-disaster Forest Management and Bark Beetle Outbreak in Tatra National Park, Slovakia. Mt Res Dev 34: 326–335.

Økland B, Netherer S, Marini L (2015) The Eurasian spruce bark beetle – role of climate. The Eurasian spruce bark beetle: The role of climate. In: Bjorkman C, Niemela P (eds) Climate Change and Insect Pests. CABI Climate Change Series 7, Wallingford UK, pp 202–219.

Pokorný J (2011) Co dokáže strom. In: Kleczek J (ed) Voda ve vesmíru, na zemi, v životě a v kultuře. Radioservis Praha, pp 429–431. In Czech.

Schwarz JD (2013) Clearing forest may transform local and global climate. Scientific American, March 4.

Šantrůčková H, Vrba J et al. (2010) Co vyprávějí šumavské smrčiny: průvodce lesními ekosystémy Šumavy. Správa Národního parku a Chráněné krajinné oblasti Šumava. In Czech.

Šíp M (2004) Remote sensing and its application in the public relations work of the national parks Bayerischer Wald and Šumava. Aktuality šumavského výzkumu II: 306–310.

Tesař M, Šír M, Zelenková E (2004) Vliv vegetace na vodní a teplotní režim tří povodí ve vrcholovém pásmu Šumavy. Aktuality šumavského výzkumu II: 84–88. In Czech.

Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. Forest Ecol Manag 202: 67–82.

Zahradník P (2004) Ochrana smrčin proti kůrovcům. Lesnická práce, Kostelec nad Černými lesy. In Czech.

COMPARISON OF PRECIPITATION AND TEMPERATURE REGIME IN THE ŠUMAVA NATIONAL PARK AND IN THE SURROUNDING FOOTHILLS

KAROLÍNA BÍLÁ[1,*], JIŘÍ HOSTÝNEK[2], and PAVEL KINDLMANN[1,3]

[1] Department of Biodiversity Research, Global Change Research Institute CAS, Bělidla 986/4a, 60300 Brno, Czech Republic
[2] Czech Hydrometeorological Institute, Mozartova 1237/41, 32300 Plzeň, Czech Republic
[3] Institute of Environmental Studies, Charles University, Benátská 2, 12801 Prague 2, Czech Republic
* Corresponding author: kcerna@volny.cz

ABSTRACT

The IPCC IS92a scenario predicts climate changes including within-year fluctuations in precipitation and a temperature increase of 1.7 °C by the year 2050 and a further 2.7 °C by the year 2100. We attempted to detect these changes in the Šumava Mts. and compare them with climate changes in the surrounding foothills. We used meteorological data records for the years 1961-2017, provided by the Czech Hydrometeorological Institute (CHMI). We recorded a decrease in precipitation, including snow cover, in the mountains and in the foothills during the last 15-20 years. Air temperature has also increased significantly in spring and summer over the last two decades. We assume that the increase in spring temperature negatively affects snow cover and causes it to melt earlier. We found that all these changes affect both the Šumava National Park and the surrounding foothills at the same rate; as a result, natural disturbances such as windstorm and bark beetle infestations occur more often and are more severe in both areas. Thus, changes in temperature and precipitation must be also considered in future management planning.

Keywords: climate change; foothills; forest management; mountains; rainfall; snow cover; Šumava

Introduction

Temperature is predicted by the IPCC IS92a scenario to increase by 1.7 °C by the year 2050 and a further 2.7 °C by the year 2100 (Mitchell 1995). Air warming is accompanied by a hydrological cycle with increases in precipitation and evaporation rates, which are slightly delayed after air temperature increases. Moreover, changes in precipitation are predicted with shifts in inter-annual variability, e.g. summer floods or less snow cover (Barry 1992). Inter-annual variability changes can also cause a decrease of soil moisture. However, this effect is regionally dependent on differences in soil structure (Boer et al. 2000).

Rainfall and runoff were intensively discussed in the Czech Republic, approximately from the beginning of the 21st century, when this country experienced devastating floods. Besides climate warming, anthropogenic pressure also results in changes in landscape and weather and negative effects are monitored not only in lowlands but also in foothill areas and mountains (Kliment and Matoušková 2009). Many studies mention changes in land-cover as one of the consequences of human activity and changes in runoff and temperature, particularly on deforestation and afforestation (Hais and Pokorný 2004; Šantrůčková et al. 2010; Pokorný and Hesslerová 2011; Kindlmann et al. 2012; Bernsteinová et al. 2013; Bílá 2016).

In forested landscapes, an increase in temperature together with a decrease in precipitation can affect tree vitality or enhance insect population growth (Seidl et al. 2011) and thus cause trees to die (Hais and Kučera 2008; Bentz 2010; Bečka and Beudert 2016). There are insects spreading northwards, which may have a major effect on mature Norway spruce (*Picea abies* (L.) Karst.) forest in the Šumava Mts. Water fluxes (evapotranspiration or runoff) probably decrease as a result of a large forest dying (Beudert et al. 2007; Adams et al. 2012). This raises a question: are bark beetles (*Ips typographus* L.) responsible for changes in weather and water regimes?

Non-intervention areas in the Šumava National Park and subsequent proliferation of bark beetle there, especially during the period 2007–2012 (following the hurricane Kyrill), are often considered as causing a decrease in precipitation, increase in temperature and decrease of snow cover because of the intensive spruce tree dieback due to bark beetle. To test this, we determined whether there is a difference in the trends in precipitation, temperature and snow cover between the Šumava Mts. and adjacent foothills over the period 1961–2017.

Methods

Study area

The area studied is located on the Czech/German border. The Šumava National Park is situated on the Czech side and Bavarian forest National Park on the German side. The Czech Hydrometeorological Institute (CHMI) is responsible for maintaining meteorological stations and keeping records of meteorological data in the Czech Republic. We selected 9 meteorological stations in the Šumava NP: Horní Planá, Lenora, Borová Lada, Kvilda, Filipova Huť, Prášily, Churáňov, Železná Ruda and Špičák, and 7 in the adjacent foothills: Ktiš, České Budějovice, Husinec, Vlkonice, Temelín, Strakonice and Klatovy (Fig. 1). We have chosen the latter set
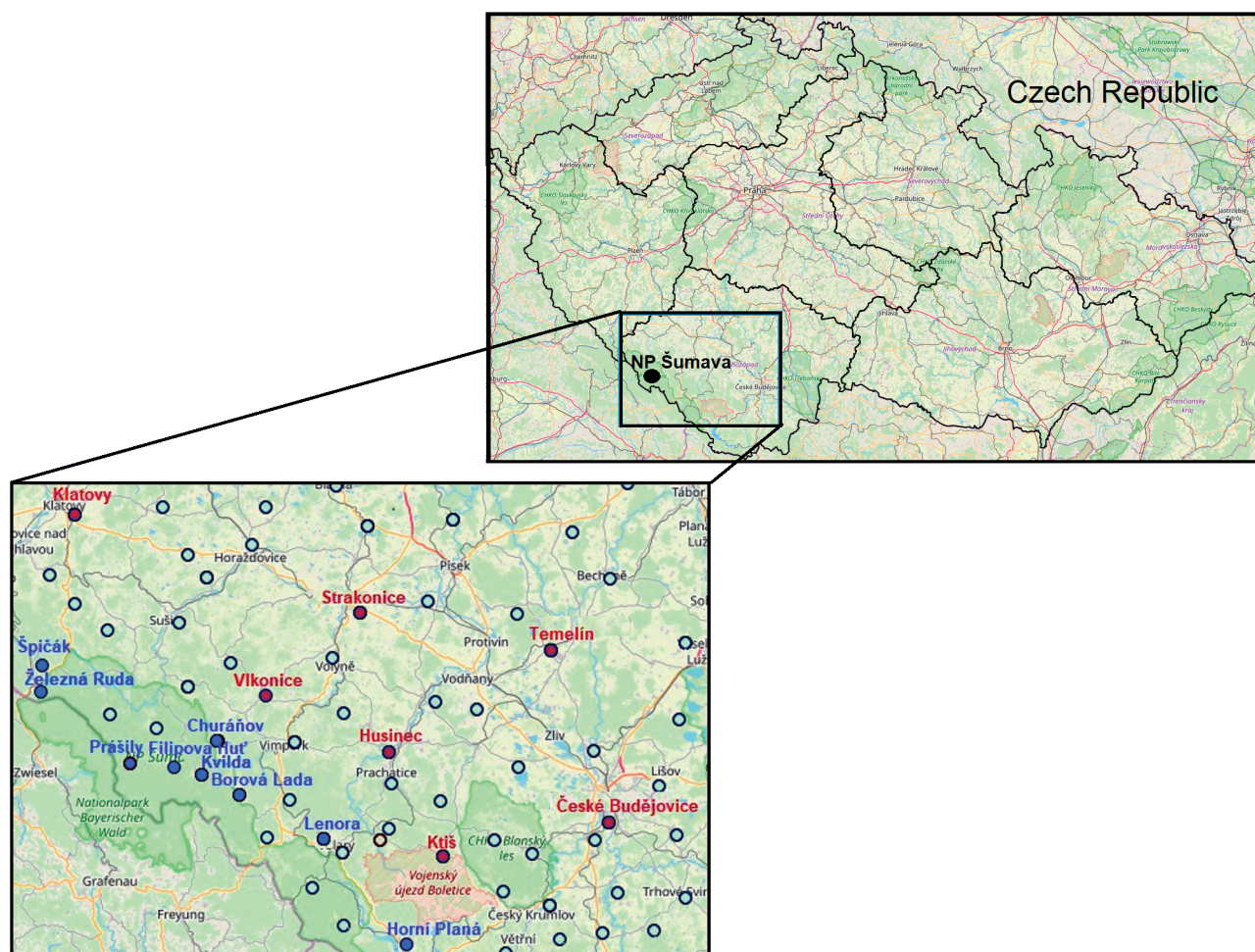
Fig. 1 Locations of the meteorological stations in the Šumava Mts. (blue): Horní Planá, Lenora, Borová Lada, Kvilda, Filipova Huť, Prášily, Churáňov, Železná Ruda and Špičák, and in the adjacent foothills (red): Ktiš, České Budějovice, Husinec, Vlkonice, Temelín, Strakonice and Klatovy. Empty circles are other CHMI meteorological stations.

of meteorological stations in such a way that they uniformly covered a vast area adjacent to the Šumava NP, to exclude the possibility of neighbourhood effect on the analyses. We used meteorological data from all these stations for the years 1961–2017 with minor gaps, with particular emphasis on precipitation, snow cover and air temperature in order to identify yearly and seasonal changes and compare the climate in the mountains with that in the adjacent foothills.

Data analyses

Precipitation analyses are based on monthly mean values. We focused on the seasonal changes during the years 1961–2017. We also compared maximum snow cover and temperature fluctuations over the same period. All the data gaps were filled using the normal ratio method and data from nearby stations. Analyses were performed in MS Excel including XLSTAT (XLSTAT 2017). Fluctuations in the data were fitted by a polynomial function (precipitation and snow cover) or linear function (temperature) and the Mann-Kendall test and the Sen's slope estimates (Kendall 1975; Yue and Wang 2004) was used to determine the strength of the detected trends.

Results

The trends recorded in precipitation and temperature are shown in Figs. 2 and 4, based on the monthly mean values per season: winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November). A polynomial function was used to fit the fluctuations in precipitation and a linear trend line to fit the temperatures recorded from 1961–2017. Fig. 2 shows historical precipitation change in year 2000 thus we further focused on decrease in precipitation in years 2000–2017 and determined the strength of these trends using a Mann-Kendall test and the Sen's slope estimates (Fig. 3, Table 1). Fig. 4 shows a linear trend in temperature increase during the whole studied period 1961–2017 and the strength of these trends was also determined using a Mann-Kendall test and the Sen's slope estimates (Fig. 5, Table 2). Similarly, we tested the changes in maximum yearly snow cover from 1961–2017 (Fig. 6) and the trend strength from the evident historical change in year 2000, i.e. from years 2000–2017 (Fig. 7, Table 3).
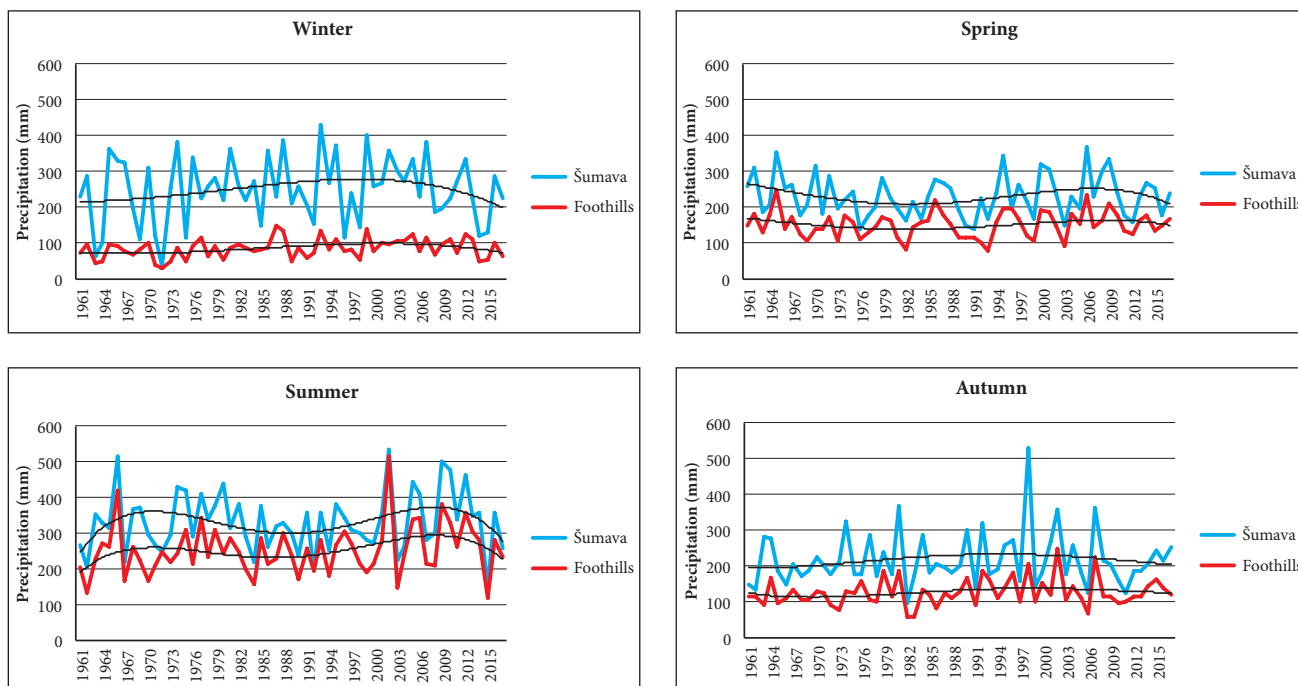
Fig. 2 Seasonal changes in precipitation recorded in the Šumava Mts. and surrounding foothills during the years 1961–2017 fitted by a polynomial function.
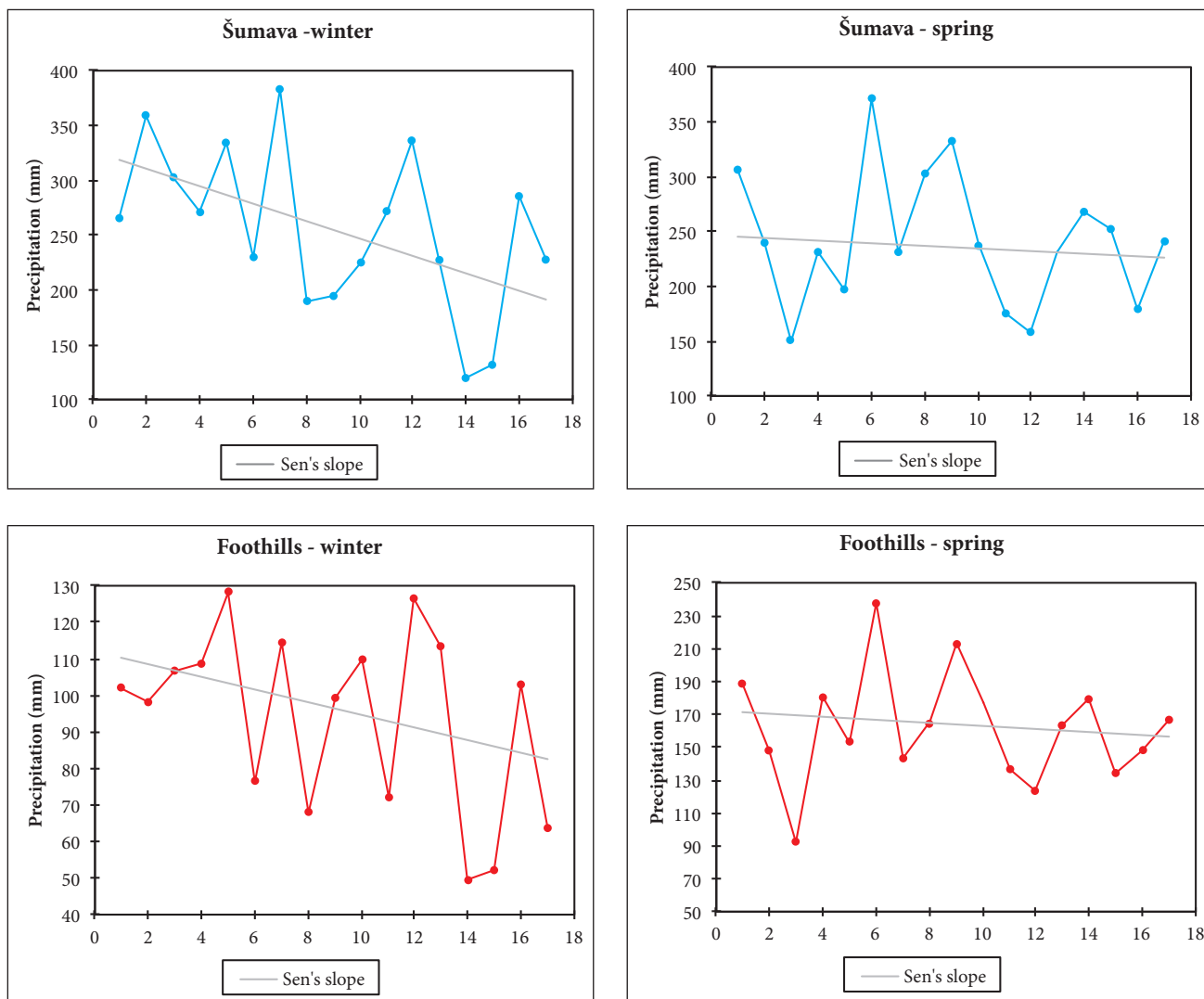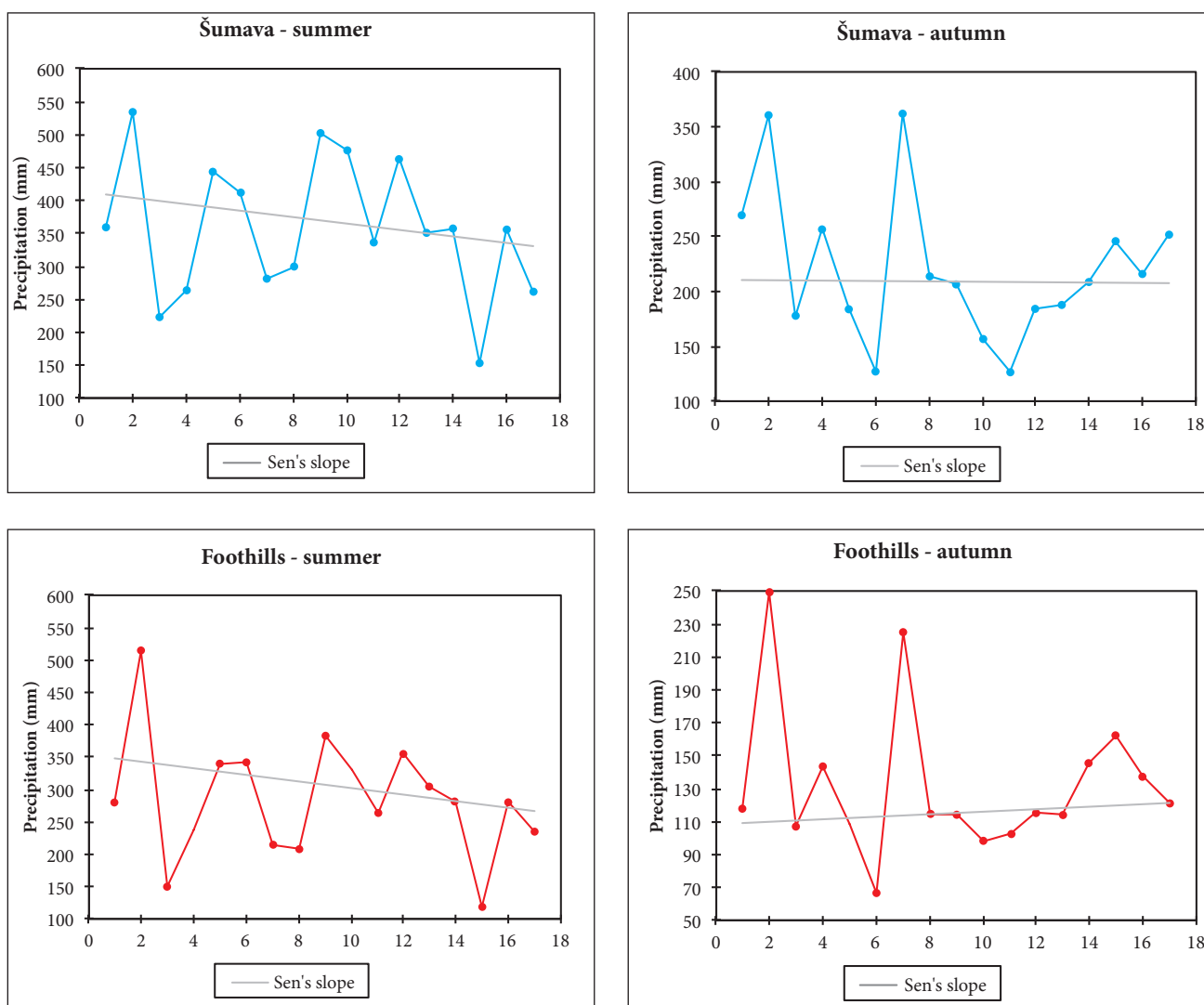
Fig. 3 Trends in precipitation recorded in the Šumava Mts. and surrounding foothills during the years 2000–2017 fitted by a linear function.

Table 1 Trends in precipitation recorded in the Šumava Mts. and surrounding foothills during the years 2000–2017 tested using a Mann-Kendall two-tailed test.

Season	winter		spring		summer		autumn	
Locality	Šumava	Foothills	Šumava	Foothills	Šumava	Foothills	Šumava	Foothills
Kendall's tau	−0.265	−0.191	−0.088	−0.118	−0.118	−0.118	0	0.103
S	−36.0	−26.0	−12.0	−16.0	−16.0	−16.0	0.0	14.0
Var(S)	589.3	589.3	589.3	589.3	589.3	589.3	589.3	589.3
p-value	0.149	0.303	0.650	0.537	0.537	0.537	1.000	0.592
alpha	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05

There was a decline in precipitation starting in 2000, particularly during winter. However, no result was significant, including the winter decline recorded in the Šumava Mts.: p-value = 0.149 on the foothills: p-value = 0.303. On the other hand, from 2000 onwards, temperature in winter (Šumava: p-value = 0.025, foothills: p-value = 0.059), spring and summer increased significantly (p-values < 0.0001). There were also significant negative trends in snow cover from 2000 onwards (Šumava: p-value = 0.029, foothills: p-value = 0.035).

Discussion

The trends of precipitation, including snow cover, show a decrease during the last 15–20 years. However, we also detected an increase in precipitation in spring and summer around the year 2000. These fluctuations and their inter-annual variability are clearly documented by the summer floods that affected the Czech Republic in 1997 and 2002. The changes in precipitation follow significant rises in temperature in spring and summer re-
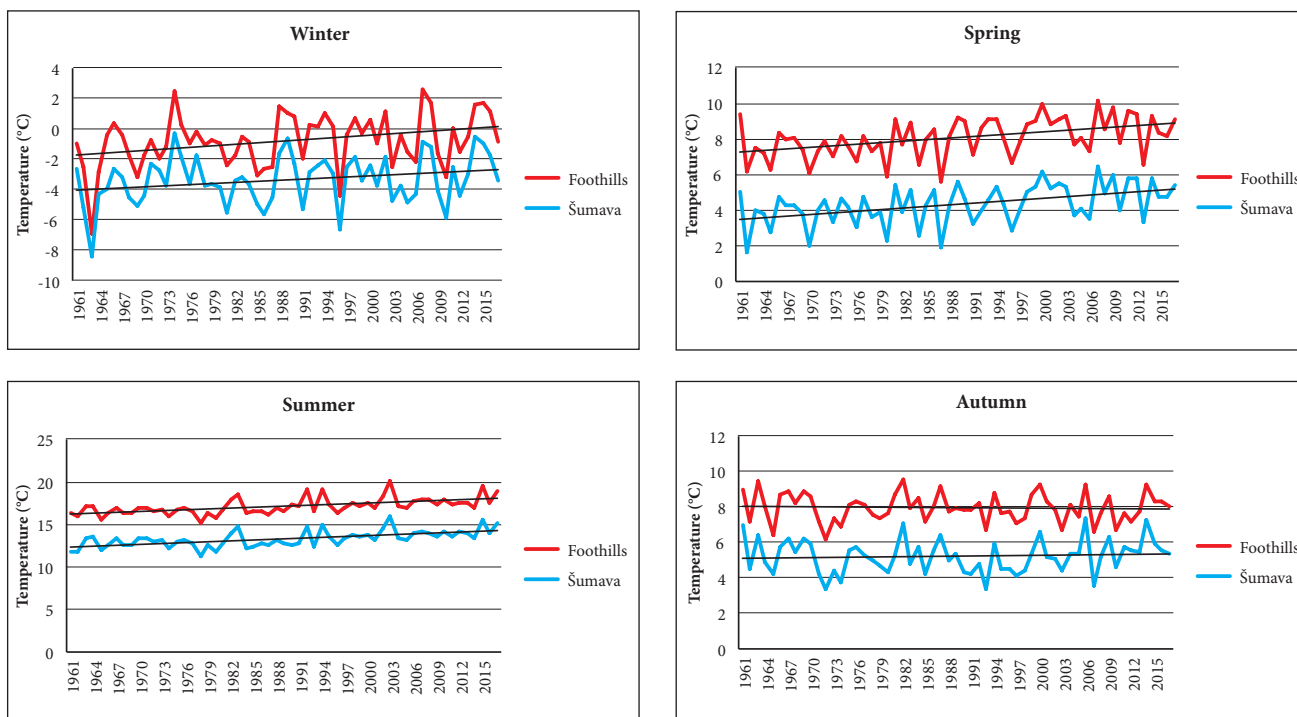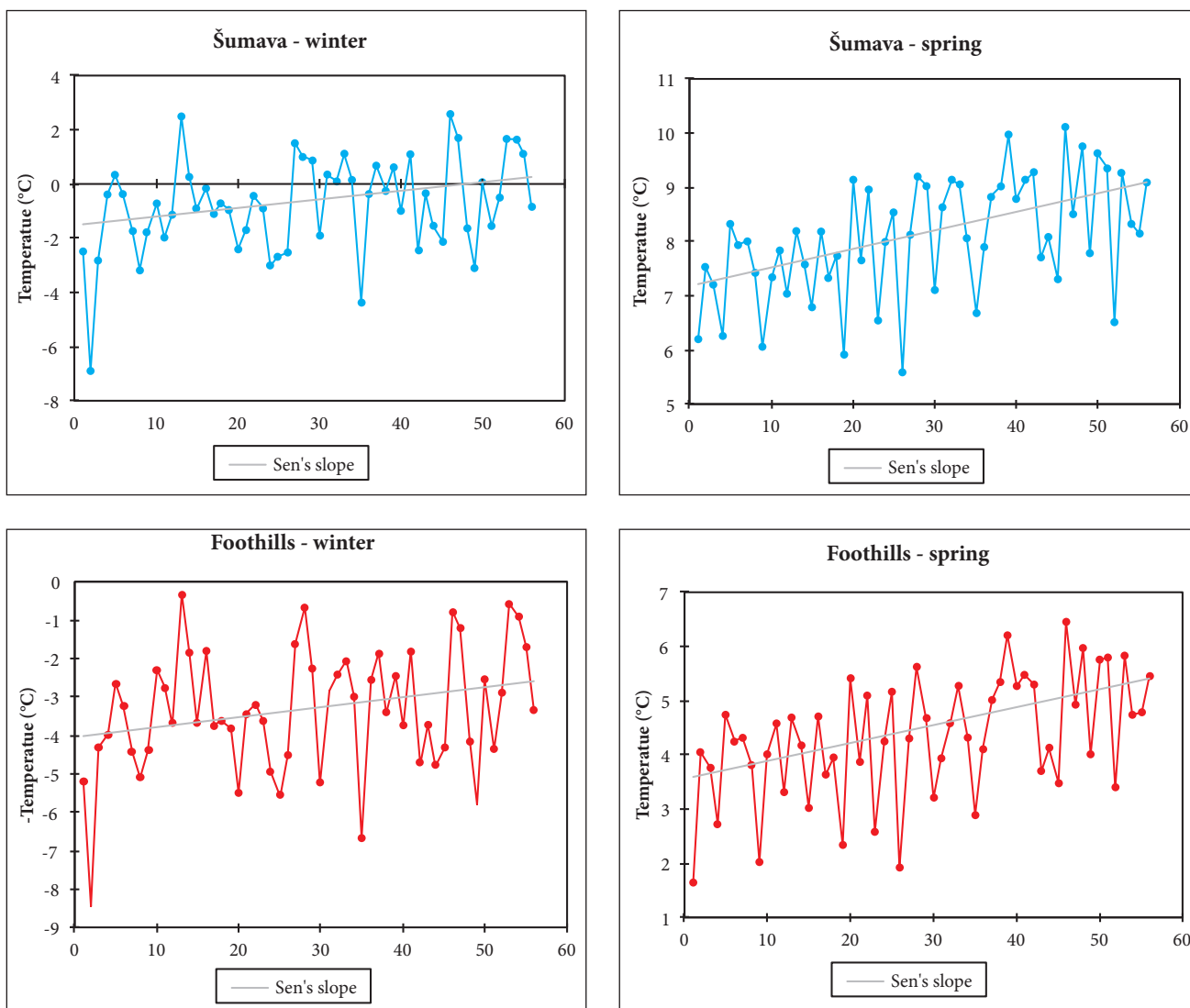
Fig. 4 Seasonal changes in temperature recorded in the Šumava Mts. and surrounding foothills during the years 1961–2017 fitted by a linear function.
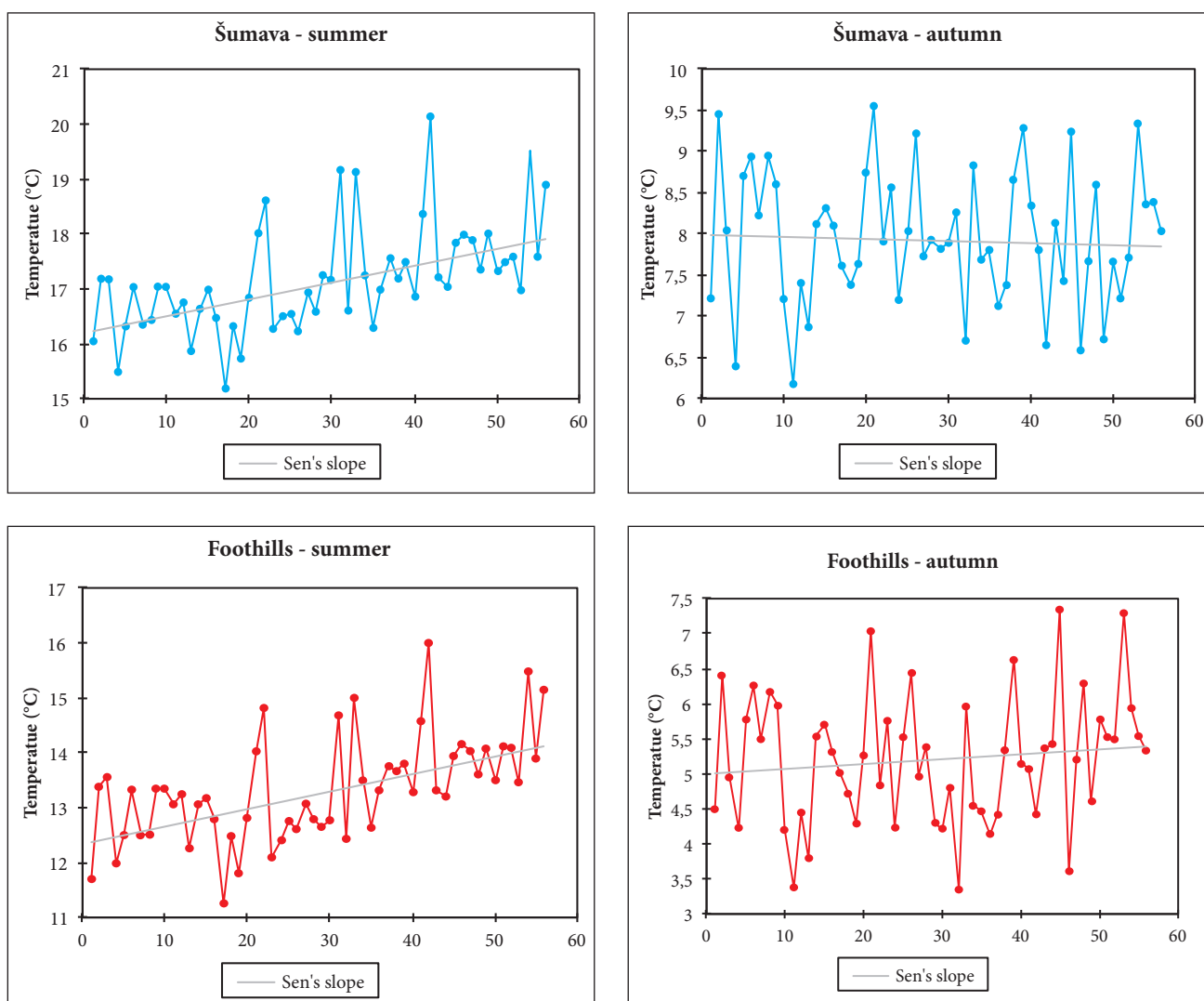
Fig. 5 Trends in temperature recorded in the Šumava Mts. and surrounding foothills during the years 1961–2017 fitted by a linear function.

Table 2 Trends in temperature recorded in the Šumava Mts. and adjacent foothills during the years 1961–2017 tested using a Mann-Kendall two-tailed test.

Season	winter		spring		summer		autumn	
Locality	Šumava	Foothills	Šumava	Foothills	Šumava	Foothills	Šumava	Foothills
Kendall's tau	0.207	0.173	0.351	0.342	0.438	0.412	−0.025	0.084
S	318.0	267.0	540.0	526.0	675.0	634.0	−39.0	130.0
Var(S)	20018.0	20017.0	20020.0	20020.0	20019.0	20014.0	20019.0	20020.0
p-value	0.025	0.059	0.000	0.000	<0.0001	<0.0001	0.783	0.358
alpha	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05

corded over the last decades. This warming is also causing changes in snow cover and result in it melting earlier in the season. It is likely that total precipitation and snow cover were lower over approximately the last 20 years in the mountains and adjacent foothills.

However, our data do not support the hypothesis that there is a significant difference in the trends in precipitation, temperature or snow cover between the Šumava NP and adjacent foothills, neither over the period 1961–2017, nor over the period 2000–2017, as is clearly seen from the figures and Sen's slope values. Thus, the claims that the

non-intervention areas in the Šumava National Park and subsequent proliferation of bark beetle there, especially during the period 2007–2012, following the hurricane Kyrill, are causing a decrease in precipitation, increase in temperature and decrease of snow cover because of the intensive spruce tree dieback due to bark beetle, are not supported by available meteorological data.

The changes in climate also altered hydrological processes in this area and affected forest stands on the summits of the mountains (Kliment and Matoušková 2009; Bernsteinová et al. 2015; Langhamer et al. 2015). These
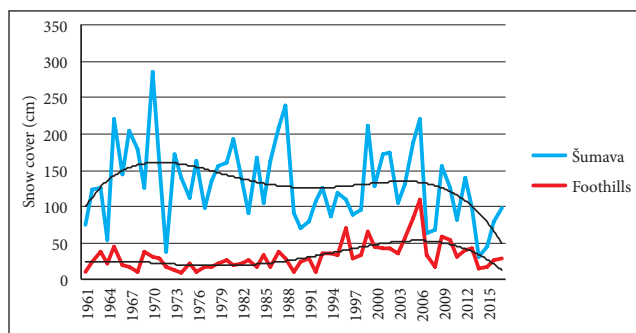
Fig. 6 Changes in snow cover (maximum snow cover/year) recorded in the Šumava Mts. and adjacent foothills during the years 1961–2017 fitted by a polynomial function.
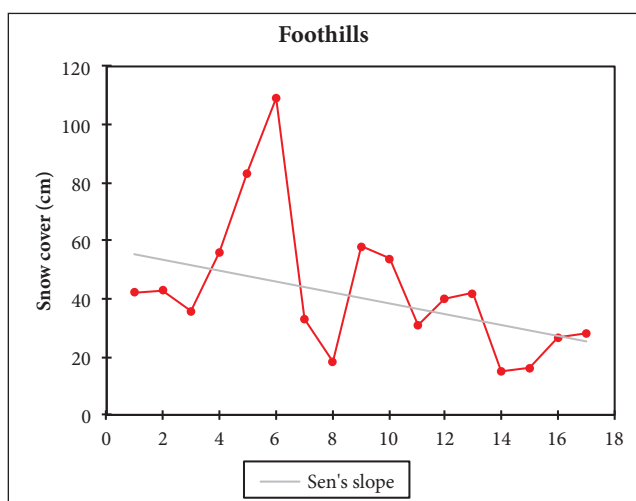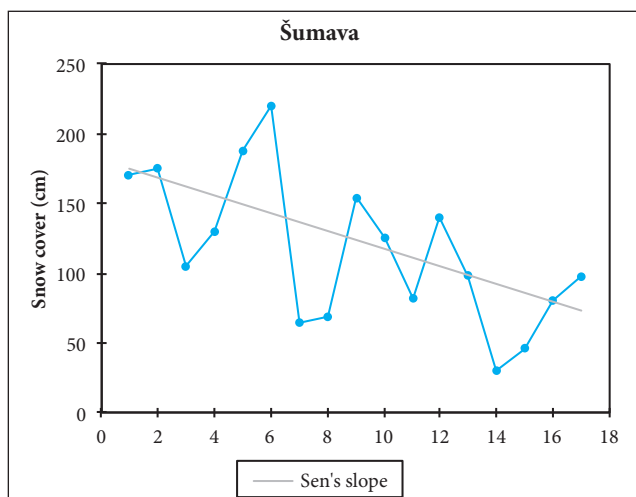
Fig. 7 Changes in snow cover (maximum snow cover/year) recorded in the Šumava Mts. and surrounding foothills during the years 2000–2017 fitted by a linear function.

Table 3 Trends in yearly snow cover recorded in the Šumava Mts. and surrounding foothills during the years 2000–2017 tested using a Mann-Kendall two-tailed test.

Locality	Šumava	Foothills
Kendall's tau	−0.39115	−0.376
S	−53.0	−51.0
Var(S)	588.3	588.3
p-value	0.029	0.035
alpha	0.05	0.05

summits are covered with Norway spruce, which is very vulnerable to even slight droughts and devastating windstorms, which occurred in 1976, 1979, 1984, 1985, 1990, 2003, 2006, 2007 and 2008, followed by bark beetle attacks in the years 1945–1952, 1983–1988, 1992–1996, 2003–2010 and 2015– to now, which were closely monitored (Hošek 1981; Skuhravý 2002; Simanov 2014).

There have been long debates among scientists and politicians on how to protect natural forests and conserve valuable mountainous habitats and their biodiversity (Hais and Pokorný 2004; Jonášová and Prach 2004; Hojdová et al. 2005; Schwarz 2013; Bílá 2016). There are two main opinions: clear fell infected trees and remove them from the site or leave the dead forest on the site and leave it to spontaneously regrow. Making the right decision is not easy when large areas of forest are killed as the change quickly becomes obvious, within a few years. However, the type of forest needs to be distinguished before applying a specific type of forest management; either it is a forest planted for economic purposes or it is a natural forest within the national park, which is protected for its natural processes including regeneration after disturbance (Kindlmann and Křenová 2016). Although the change in climate is obvious and similar in both the Šumava NP and the surrounding foothills, spontaneous forest succession has already commenced in the vast area attacked by bark beetles (Bentz et al. 2010; Šantrůčková et al. 2010; Kindlmann et al. 2012; Økland 2015).

Climate changes are a common phenomenon in the Earth's history and people must learn how to react to them. During the past decades, weather monitoring techniques have improved greatly and we are able to predict future scenarios more precisely. The forecast is of increasing temperature and decreasing precipitation, which will significantly influence water supplies. It is advantageous to forecast these changes in time and carry out corresponding steps to adapt to such environmental changes.

Acknowledgements

REFERENCES

Adams HD, Luce CH, Breshears DD, Allen CD, Weiler M, Hale VC et al. (2012) Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. Ecohydrology 5: 145–159.

Barry RG (1992) Mountain weather and climate, 2nd edn. Routledge, London, New York.

Bečka P, Beudert B (2016) Kůrovec a voda. Jak bezzásahovost ovlivňuje vodní režim na Šumavě. Šumava, jaro: 16–17. In Czech. In Czech.

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

Bernsteinová J, Bässler C, Zimmermann L, Langhammer J, Beudert B (2015) Changes in runoff in two neighbouring catchments in the Bohemian Forest related to climate and land cover changes. J Hydrol Hydromech 63: 342–352.

Bílá K (2016) Are bark beetles responsible for drouhgts in the Šumava Mts.? Eur J Environ Sci 6: 108–113.

Beudert B, Klöcking B, Schwarze R (2007) Große Ohe. Impact of bark beetle infestation on the water and matter budget of a forested catchment. In: Puhlmann H, Schwarze R (eds) Forest hydrology – results of research in Germany and Russia. Deutsches Nationalkomitee für das International Hydrological Programme (IHP) der UNESCO und das Hydrology and Water Resources Programme (HWRP) der WMO. IHP/HWRP-Berichte Heft 6, Koblenz.

Boer G, Flato G, Ramsden D (2000) A transient climate change simulation with greenhouse gas and aerosol forcing: projected climate to the twenty-first century. Climate Dynamics 16: 427–450.

Hais M, Kučera T (2008) Surface temperature change of spruce forest as a result of bark beetle attack: Remote sensing and GIS approach. Eur J Forest Res 127: 327–336.

Hais M, Pokorný J (2004) Changes in land cover temperature and humidity parameters resulting from spruce forests decay. Aktuality šumavského výzkumu II: 49–55. In Czech.

Hojdová M, Hais M, Pokorný J (2005) Microclimate of a peat bog and of the forest in different states of damage in the National Park Šumava. Silva Gabreta 11: 13–24.

Hošek E (1981) Studie o výskytu kalamit na území ČSR od roku 1900: Brandýs nad Labem: Lesprojekt 10-12: 8–86. In Czech.

Jonášová M, Prach K (2004) Central-European mountain spruce forests: regeneration of tree species after a bark beetle outbreak. Ecol Eng 23: 15–27.

Kendall MG (1975) Rank correlation methods. Griffin, London.

Kindlmann P, Křenová Z (2016) Biodiversity: Protect Czech park from development. Nature 531: 448.

Kindlmann P, Matějka K, Doležal P (2012) Lesy Šumavy, lýkožrout a ochrana přírody. Karolinum, Praha. In Czech.

Kliment Z, Matoušková M (2009) Runoff Changes in the Šumava Mountains (Black Forest) and the Foothill Regions: Extent of Influence by Human Impact and Climate Change. Water Res Manag 23: 1813–1834.

Langhammer J, Su Y, Bernsteinová J (2015) Runoff Response to Climate Warming and Forest Disturbance in a Mid-Mountain Basin. Water 7: 3320–3342.

Mitchell JFB, Johns TC, Gregory JM, Tett SFB (1995) Climate response to increasing levels of greenhouse gases and sulphate aerosols. Nature 376: 501–504.

Økland B, Netherer S, Marini L (2015) The Eurasian spruce bark beetle: The role of climate. In: Björkman C, Niemelä P (eds) Climate Change and Insect Pests. CABI Climate Change Series, UK, pp 202–219.

Pokorný J, Hesslerová P (2011) Odlesňování a klima. Klimatické změny v Mau Forest v západní Keni. Vesmír 90: 573–578. In Czech.

Šantrůčková H, Vrba J et al. (2010) Co vyprávějí šumavské smrčiny: průvodce lesními ekosystémy Šumavy. Správa Národního parku a Chráněné krajinné oblasti Šumava. In Czech.

Schwarz J (2013) Clearing forest may transform local and global climate. Scientific American, March 4.

Seidl R, Schelhass MJ, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biol 17: 2842–2852.

Simanov V (2014) Kalamity v historii a současnosti. Lesnická práce 93: 573–575. In Czech.

Skuhravý V (2002) Lýkožrout smrkový a jeho kalamity. Praha, Agrospoj. In Czech.

XLSTAT (2017) Data Analysis and Statistical Solution for Microsoft Excel. Addinsoft, Paris, France.

Yue S, Wang CY (2004) The Mann–Kendall test modified by effective sample size to detect trend in serially correlated hydrological series. Water Res Manag 18: 201–218.