

MODIS-based vegetation index has sufficient sensitivity to indicate stand-level intra-seasonal climatic stress in oak and beech forests

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MODIS-based vegetation index has sufficient sensitivity to

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2 indicate stand-level intra-seasonal climatic stress in oak and beech

3	forests								
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16									
17	Abstract								
18	Context: Variation in photosynthetic activity of trees induced by climatic stress can be								
19	effectively evaluated using remote sensing data. Although adverse effects of climate on								
20	temperate forests have been subjected to increased scrutiny, the suitability of remote								
21	sensing imagery for identification of drought stress in such forests has not been explored								
22	fully.								
23	Aim: To evaluate the sensitivity of MODIS-based vegetation index to heat and drought								
24	stress in temperate forests, and explore the differences in stress response of oaks and								
25	beech.								
26	Methods: We identified 8 oak and 13 beech pure and mature stands, each covering								
27	between 4 and 13 MODIS pixels. For each pixel, we extracted a time series of MODIS								
28	NDVI from 2000 to 2010. We identified all sequences of continuous unseasonal NDVI								
29	decline to be used as the response variable indicative of environmental stress. Neural								

30	Networks-based regression modelling was then applied to identify the climatic variables
31	that best explain observed NDVI declines.
32	Results: Tested variables explained 84–97% of the variation in NDVI, whilst air
33	temperature-related climate extremes were found to be the most influential. Beech
34	showed a linear response to the most influential climatic predictors, while oak responded
35	in a unimodal pattern suggesting a better coping mechanism.
36	Conclusions: MODIS NDVI has proved sufficiently sensitive as a stand-level indicator
37	of climatic stress acting upon temperate broadleaf forests, leading to its potential use in
38	predicting drought stress from meteorological observations and improving
39	parameterisation of forest stress indices.
40	Key words: drought stress, heat stress, NDVI, regression modelling, temperate forest,
41	neural networks
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43	Executive summary
44	This study explores the suitability of MODIS satellite imagery for the detection of intra-
45	seasonal heat and drought stress in temperate forests. It is clear that this data can provide
46	valuable information complementary to forest stand-based ecophysiological research and
47	allows for the quantification of inter-specific differences in stress response.

Introduction

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The effect of extreme climate events on terrestrial ecosystems is being increasingly recognized as one of the first signs of impending climate change (Allen et al. 2010; Leuzinger et al. 2005). Survival of woody species within their present range is likely to be constrained by water availability, prolonged drought during vegetation season may induce episodes of large-scale tree decline (Allen et al. 2010; McDowel et al. 2011). Drought induced tree mortality has mainly been observed in the Mediterranean region, affecting a range of species (for an overview see Allen et al. 2010). Further north, lack of water has been identified chiefly as a predisposing factor for biotic stressors, for example drought periods repeatedly triggering large-scale pest outbreaks (Rouault at al. 2006). In temperate forests, repeated episodes of drought usually cause a decrease in leaf area index (Le Dantec et al. 2000), often resulting in a decline in forest productivity (Glenn et al. 2008, Hlásny et al. 2011a). However, some recent observations such as drought induced mass beech mortality (Lakatos and Molnár 2010) or drought-triggered pest outbreaks (Mátyás et al. 2010) indicate the importance of drought as an emerging primary mortality agent in temperate Europe. This link is underlined by the presence of drought sensitive xeric limit of several temperate tree species, as well as by projections indicating drought induced retreat of some species (Czúcz et al. 2011, Hlásny et al. 2011a). European beech (Fagus sylvatica) and several oaks (Quercus sp.) overlap to a certain extent and together they constitute some of the ecologically and economically most important species. Oaks are favoured by a relatively warm and dry climates (Czúcz et al. 2011; Epron and Dreyer 1993), while beech has been identified as sensitive to drought and potentially vulnerable to climate change (Geßler et al. 2007; Mátyás et al. 2010; Leuzinger et al. 2005). Since climate change may force a replacement of beech by oaks in some localities, the competitiveness and stress tolerance of beech and various oak species is being

73	increasingly recognized as central to future-proofing broadleaf temperate forests
74	(Leuschner et al. 2001; Raftoyannis and Radoglou 2002; Scharnweber et al. 2011).
75	Traditionally, the frequency and severity of drought has been evaluated by drought
76	indices calculated from meteorological observations (Vicente-Serrano et al. 2012). Since
77	forests are sparsely covered by meteorological stations (Caccamo et al. 2011), this
78	approach does not allow for a reliable drought assessment of a large area or in a varied
79	landscape. Variations in photosynthetic activity induced by climatic or other stress can,
80	however, be effectively evaluated using remote sensing data (Glenn et al. 2008; Lobo et
81	al. 2010). Fine spectral resolution in the water sensitive part of the electromagnetic
82	spectrum makes MODIS sensor (Moderate Resolution Imaging Spectroradiometer,
83	NASA) outstandingly suitable for drought monitoring (Ceccato et al. 2001). During the
84	MODIS mission (from 2000 onwards), the instrument has generated large amounts of
85	data used for monitoring of drought and water availability at global to regional scales. To
86	date, however, few studies have explored the utility of MODIS-type data to monitor
87	drought in forested areas (Caccamo et al. 2011; Vacchiano et al. 2012; Wang et al. 2009),
88	with Central Europe not covered at all. Spectral reflectance data are usually compressed
89	into vegetation indices. One such index, the widely used Normalised Difference
90	Vegetation Index (NDVI), exploits the variation in the absorption of photosynthetically
91	active radiation by living plant foliage (Myneni and Williams 1994). Since photosynthetic
92	activity is limited by resource availability, NDVI has also been used to investigate the
93	incidence and severity of drought (Caccamo et al. 2011; Ji and Peters 2003).
94	In the present study, we investigate the usability of MODIS-NDVI as an indicator of the
95	severity of vegetation stress resulting from a potential water deficit and excessive
96	temperatures in mature beech and oak stands in Central Europe. We hypothesize that (i)
97	specific stress episodes can be identified in time series of MODIS-NDVI localised to

forest stands, and (ii) these patterns are linked to specific intensity and duration of rainless and heat periods. We perform a regression modelling analysis to assess the usefulness of MODIS imagery for investigations of intra-seasonal variation of forest vigour and to identify environmental variables which best predict the stress response of beech and oak stands.

1. Materials and methods

2.1 Study region and experimental plots

The research focuses on the territory of Slovakia (Central Europe) where a number of forest plots distributed across the whole country were identified. Forest management plans and other databases archived by the National Forest Centre, Slovakia, were used to localise experimental plots using criteria listed in Table 1.

Table 1

The purpose of stand selection was to create a database of mature and homogenous oak and beech stands seamlessly covering groups of MODIS pixels (250×250 m, see Appendix A). Oak stands contained mixtures of Sessile oak (*Quercus petrea*), Pedunculate oak (*Quercus robur*) and Pubescent oak (*Quercus pubescens*). Only single-layer stands with closed canopy were considered for this study. Each selected stand was composed of at least 99% of the target species. This threshold was set arbitrarily high to allow for a reasonable confidence in inter-specific comparison. To reduce the variability of potential stress responses, we used digital forest soil maps to exclude forest stands on soils with extremely low or high water holding capacity. As a result, the only soil type under the final selection of stands is sandy loam or loam of medium depth (ca. up to 120 cm in oak plots) or medium-to-high depth (ca. up to 200 cm in beech plots).

122 In total, 13 beech experimental plots covered by a total of 66 MODIS pixels, and 8 oak 123 plots covered by 55 MODIS pixels met the selection criteria (Fig. 1, Table 2). 124 Fig. 1 Table 2 125 126 127 2.2 Time series of MODIS-NDVI 128 NDVI is an approximately linear estimate of the fraction of photosynthetically active 129 radiation (PAR) intercepted by photosynthesizing tissue of vegetation, provided that 130 certain constraints on background, solar and view angles, and atmospheric transparency are fulfilled (Myneni and Williams 1994). NDVI is formulated as: 131 132 NDVI = $(\rho NIR - \rho Red)/(\rho NIR + \rho Red)$ 133 Eq. 1 134 135 where pNIR and pRed are reflectance values of near infrared and red radiation. 136 Hence, NDVI theoretically takes on values between -1 and 1, with values approaching 1 137 indicating high density of green leaves with good photosynthesizing performance. 138 For the purpose of this study, NDVI images with spatial resolution 250×250 m covering 139 the period 2000-2010 were derived from MODIS product MOD09GQ (Source: NASA 140 LP DAAC). Despite potentially adverse effect of anisotropical reflectance of vegetation on the use of daily MODIS data (e.g. Shuai et al. 2013), we made preference for this 141 142 product over 16-day products with 500 m resolution which are free of this potentioal 143 source of error. Since we strive to focus on the immediate vegetation dynamics at daily scale in the varied landscape of Central Europe, the spatial resolution of used imagery can 144 critically limit the usability of such imagery. Indeed, Franch et al. (2013) suggested that 145

errors due to the Lambertian assumption in daily MODIS data are likely to be negligible in case of NDVI values. Since clouds and atmospheric aerosols can introduce substantial noise in MODIS NDVI data (Wang et al. 2003, Hmimina et al. 2013), a two-step quality control has been applied to remove observations contaminated by atmospheric or other interference. First, MOD09GA (500x500) product was used to exclude images taken under high sensor zenith angles, and pixels contaminated by clouds and aerosols. Despite lower resolution, MOD09GA is better suited for this step than MOD09GQ with 250 m resolution, since the latter product does not contain information on pixel contamination by aerosols. Moreover, MOD09GA contains information detected in all spectral bands of MODIS (range 459–2,155 nm), supporting its superior performance in the detection of contaminated pixels. Indeed, cloud masks based on this product have been shown to slightly overestimate real clouding (Kotarba et al. 2009). Despite a very conservative first step, a portion of noise can remain in the data even after the quality assurance image was applied (Hmimina et al. 2013, Wang et al. 2003). Therefore, we applied a follow-up manual quality control procedure aimed at removal of NDVI values which were inconsistent with the expected annual cycle of vegetation greenness (Bruce et al. 2006).

2.3 Climate data and definition of drought and heat periods

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Daily meteorological data collected at 46 meteorological stations in the vicinity of experimental plots (Fig. 1) (Source: Slovak Hydrometeorological Institute) were used for the identification of rainless periods and periods during which daily mean or maximum air temperature exceeded selected thresholds (Table 4). Meteorological stations indicative of conditions specific to each experimental plot were selected from the national network of stations using the following criteria: horizontal and vertical distance from selected

stands (Table 1); landscape orography and climatic variability of broader surroundings. The latter two criteria were included to prevent interpolation over mountain ridges and across climatically different regions. Daily average, minimum and maximum air temperature and daily precipitation data were interpolated to the centre position of each experimental plot. A rainless period was defined as a sequence of days during which no more than 5 mm of precipitation was recorded per day. This value represents precipitation with low probability of reaching the roots due to interception loss in the canopy (van de Salm et al. 2007), as well as evaporation from the ground. Since no information on actual soil or leaf water content is available at the desired scale and terrain cover, we use the duration of rainless periods as a proxy for drought. For the sake of simplicity, we use term "drought stress" for NDVI responses induced by prolonged rainless periods, being aware of the limitations of such interpretation. A heat period was defined as sequence of days with mean or maximum air temperature exceeding arbitrarily set thresholds (Table 4). 2.4 Identification of stress episodes in MODIS-NDVI time series 2000-2010 Stress episodes were defined as continuous sequences of declining NDVI values observed during the period of full foliage. Each NDVI value pertaining to a stress episode was expressed in terms of actual decline in NDVI relative to the overall permissible decline observed in each MODIS pixel (local amplitude) and calculated according to the following formula: $NDVI_{decline} = 100 - ((NDVI_{max} - NDVI_{stress})/(NDVI_{max} - NDVI_{min}) \times 100)$ Eq. 2

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where NDVI_{max} represents the NDVI of unstressed vegetation and is calculated as the mean of 2-4 NDVI observations immediately preceding a stress episode, NDVI_{stress} is a value in a sequence of declining NDVI values, and NDVI_{min} is the lowest value of annual NDVI amplitude, correspondent with a period without foliage. NDVI_{min} was constant during the investigated 10 year period, reaching 0.52 for beech and 0.44 for oak; these values were found to be uniform across all investigated plots and in all years. The difference between NDVI_{max} and NDVI_{min} defines the local amplitude for each pixel (Fig. 2). Introducing local amplitudes allows for comparability of NDVI declines in spite of inter-annual and inter-pixel variability in NDVI_{max}. In addition, NDVI_{max} of unstressed vegetation constantly declines from spring to late summer, i.e. from ca. 1.0 to 0.9 (Soudani et al. 2012); hence the need for data standardisation. As a consequence, the local amplitude of NDVI is smaller in beech (0.52 to local maximum) than in oak (0.44 to local maximum). Only stress episodes consisting of at least 3 sequentially declining values observed in at least two MODIS pixels from each experimental plot were considered. Also, the magnitude of each decline was set to exceed 5% of local NDVI amplitude. Stress episodes were extracted manually for each pixel during the vegetative season over the entire 10-year period. The length and timing of periods of full foliage differed between years and pixels, as indicated by the seasonal course of NDVI values. The fact that only the period of full foliage was considered, together with the strict stand selection criteria described earlier, implies that forest understory and herbaceous layer should not affect the evaluated spectral response.

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2.5 Regression modelling of observed stress episodes and climate

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Three types of interaction between stress episodes and climatic extremes may occur in this type of studies; (i) climate extremes (rainless and/or heat periods) correspond with incidence of NDVI declines (True Responses, TRs), (ii) NDVI declines occur in periods when no heat and rainless period has occurred (False Responses, FRs), (iii) no NDVI decline is apparent during heat and rainless periods (False Triggers, FTs). An inclusion of FRs and FTs in the regression analysis is not possible because either the dependent or explanatory variable(s) would be missing. However, a very high occurrence of FRs and FTs in the dataset may hinder proper interpretation of results of regression modelling. To investigate this possibility, we quantified the frequency of FRs and FTs. Maximum NDVI_{decline} value observed in each stress episode (Eq. 2, Fig. 2) is used as the dependent variable and regressed against the list of explanatory variables given in Table 4. Regression modelling was run independently for the two species to facilitate an evaluation of inter-specific differences in stress response. First, bootstrap sampling was applied repeatedly to randomly split input data into training, testing, and validation sets in the ratio of 70:15:15. Then, Neural Network-based modelling was used, following the workflow described by Hlásny et al. (2011b). In total, 2,000 Neural Networks with varying architecture were trained for each species; the training represents an iterative fitting of a neural network-based model into parameterisation data while controlled by testing and validation samples. Correlation coefficients between NDVI_{decline} values predicted by trained Neural Networks and observations allocated to testing and validation sets were calculated to assess the predictive power of trained networks. Subsequently, an ensemble of 15 best-performing networks (i.e. those reaching the highest correlation coefficients between observed and predicted NDVI_{decline} values) out of the initial set of

2,000 trained networks was used to identify the most influential predictors and to rank them using the sensitivity analysis procedure.

The sensitivity analysis used in this study iteratively discards an input variable at a time and assesses overall network error. A measure of sensitivity then is the ratio of the error produced by a Neural Network with a missing variable relative to the error of a Network with the full set of input variables. The more sensitive the network is to the inclusion of a particular input, the greater the measured deterioration of prediction and therefore the greater the error ratio (1 represents a neutral relationship).

Since each of the 15 retained networks generates one set of sensitivity scores (SS), the stability of regression models in terms of prediction consistency can be tested. We used the Principal Component Analysis (PCA) to evaluate the inter-model consistency of sensitivity scores on the basis of correlation of all 15 SS sets with the Principal Component 1 (PC1); high correlations of all SS with PC1 indicate consistent signal produced by all models (Hlásny et al. 2011b). All statistical analyses were performed in Statistica Neural Networks v.10 (StatSoft Inc., 2004).

2. Results

3.1 Stress episodes

The mean length of observed continuous declines in NDVI was 10.6 days in beech and 12.5 in oak stands (P=0.023), while the longest observed period of continuous NDVI decline was 27 days in beech and 24 days in oak (see Appendix B for an example). The most severe declines of NDVI during a stress episode (NDVI_{decline}) reached 25–30% of the local NDVI amplitude in beech and 40-45% in oak stands. The variability of NDVI_{decline} was larger in oak stands; standard deviation of declines reached 57% of mean in beech and 70% in oak (Table 3). We found that each NDVI_{decline} episode was associated with a single rainless period, while several heat periods from one to several

days long occurred within its duration. None of the heat periods identified by the thresholds specified for this research (Table 4) was sufficiently long to induce an observable decline in NDVI values. Stress episodes always ended at first precipitation event which cancelled the respective rainless period. NDVI recovered to its local maximum shortly after and no irreversible changes were observed.

Table 3

As a technical verification study, we explored spectral responses of foliage to drought in the red (620-670 nm) and near infrared band (840-876 nm, Appendix C). The same bands were used to calculate NDVI values in the main objective of this manuscript (Eq. 1). Bench-top NDVI declines are mainly related to an increased reflectance in the red band, which is indicative of reduced photosynthetic performance of vegetation (i.e. lesser absorption and higher reflectance of photosynthetically active radiation, Reflectance in the near infrared band was found to increase as well, although the pattern of increase was not as clear as that of the red band. We observed more than threefold increase in the reflectance in the red band at the end of stress periods lasting from 10 to 20 days, as compared to unstressed vegetation. Increased absorption in the near infrared band, which could be indicative of drought induced changes in leave cell walls, was not observed in the current investigation.

3.2 Regression modelling

Correlations between predicted and observed values, calculated as the mean of 15 best performing networks for each tree species (Table 5) show only small inter-network variability and were very similar between training, testing and validation sets. The range of correlation coefficients between 0.84–0.97 implies stable and well performing

regression models. The coefficients suggest that explanatory variables utilised in this analysis explain a significant portion of the variability of identified stress episodes. Table 5 Sensitivity scores (SS) produced by the 15 best-performing regression models were found to be highly consistent among the models. PC1 explained 81% of the total variability of SS in beech and 76% in oaks and SS of no model differed significantly from the main pattern represented by PC1. Differences in mean sensitivity scores indicated variation in the predictive power of explanatory variables between the two tree species, suggesting diverging physiological capacity to respond to heat and drought stress (Table 6). The largest difference was observed for GDD, which was the most influential predictor in beech (SS=4.62), while occupying only the 5th position in oak (SS=1.61). The number of days with average air temperature above 24°C was the most influential variable in oak (SS=5.60), whilst in beech the number of days with maximum air temperature above 29 and 20°C were the most influential of temperature related predictors (SS=4.00 and 3.90). The duration of rainless periods was not found to affect the stress response significantly (15th order with SS=1.27 in beech, and 12th order with SS=1.32 in oak), and its importance was greatly subdued by heat-related variables. Non-climatic variables such as elevation and stand age did not affect declines of NDVI. In oaks, mean SS of the most influential variables (N-Tavg>24°C, N-Tmax>32°C, N-Tmax>29°C) differed significantly from each other, as well as from all lower-rank variables (α =0.05, Tab. 6). In beech, the decrease in SS from the first to the last-ranked variable was not so apparent, however the mean SS of the group of most influential variables was significantly different from the lower-rank variables. Table 6

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3.3 Univariate responses

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In order to understand the phenological and physiological implications of the most influential explanatory variables, we further analysed dominant relationships. Diverging response to the most influential climatic variables was found in oak, which has shown highest NDVI declines at short to medium duration of unfavourable climate, while longer duration stress events were accompanied by less severe NDVI declines. The largest decreases of NDVI were induced by 1-2 hot days accumulated during stress episodes with average daily air temperature above 24°C (the most influential variable, SS=5.60), though the variability of responses was high (Fig. 3a). Unimodal response was observed at N-Tmax>29°C (SS=2.51) with maximum NDVI declines at around 2-4 days (Fig. 3b). Linearly decreasing response was observed at N-Tmax>32°C (SS=3.18) (Fig. 3c), with extreme variability at 0 days (i.e. at NDVI declines with no observation of temperature above 32°C); the reason for this is the low number of stress episodes during which days with air temperature exceeded the threshold of 32°C. Fig. 3 In contrast to oak, increasing the severity or the duration of heat stress in beech increased the magnitudes of NDVI declines in linear fashion. The main univariate relationships between the most influential climatic variables and the stress response of beech are presented in Fig. 4. Fig. 4 The only explanatory variable to which we observed a unimodal response in both species was GDD (Fig. 3e, 4e). Interestingly, the GDD value denoting the highest NDVI sensitivity was between 900-1,000 in both beech and oak. Observed length of a drought period was not influential in either species (SS=1.27 in beech and SS=1.32 in oak), it is

however functionally associated to all observed stress episodes. A drought ends at a

precipitation event and NDVI recovers to its local and seasonal maximum shortly after. Considering it on a univariate basis indicates a linear relationship between the length of drought and corresponding magnitude of NDVI declines in beech, but a quadratic relationship in oak (Fig. 3d, 4d).

3.4 Incidence of False Responses and False Triggers

Relationships between frequencies of rainless periods longer than 4 days which were characterised by at least 3 non-declining NDVI observations and rainless periods inducing a stress response were studied. The 4-day criterion was chosen to avoid affecting the analysis by a large number (in the order of thousands) of rainless periods of short duration which are largely irrelevant for tree stress assessment. In beech, a remarkably strong prevalence of rainless periods up to 20 days long with non-declining NDVI values was identified (Fig. 5). In rainless periods longer than 20 days, however, a relatively equal frequency of FTs and TR was observed. In oaks, the frequency of FTs is substantially higher than the frequency of rainless periods inducing stress response for all durations of rainless periods.

Fig. 5

3. Discussion

4.1 Ecophysiological inference and applicability

Currently, even small changes in precipitation regime are thought to have a considerable impact on beech, raising the possibility of co-occurring species such as oak gaining a competitive advantage under projected climatic changes (Scharnweber et al. 2011).

Oaks appear to possess the capacity to better tolerate drought, an array of efficient protection mechanisms against permanent high irradiance damage under drought stress

370 has been identified (Epron and Dreyer 1993; Raftoyannis and Radoglou 2002; Wamelink 371 et al. 2009). 372 As indicated in our analysis, drought approximated by the duration of rainless periods 373 induced a reduction in photosynthetic activity indicated by NDVI in both species. 374 Observed climatic stress did not result in irreversible tree decline and mortality in either 375 species, such an event would have been evidenced by a discontinuity in the investigated 376 NDVI time series. Generally, drought-induced damage may lead to organ dysfunction, but it only seldom results in direct and immediate induction of tree decline and death 377 378 (Bréda et al. 2006). Hence, continuous decline of NDVI values in years following 379 extreme droughts is more likely to occur than intra-seasonal abrupt change not followed 380 by a recovery, as reported in France when a substantial increase in tree mortality occurred 381 in years after the 2003 heat wave (Renaud et al. 2006). 382 In this study, the variability of maximum NDVI declines was higher in oak than in beech, 383 possibly related to differences in the plasticity of response, but also the presence of 384 several oak species in oak experimental plots (Q. petrea, Q. robur, Q. pubescens). 385 Differential response of oak species to drought has been reported by Epron and Dreyer 386 (1993) or Raftoyannis and Radoglou (2002). Mean and maximum observed NDVI 387 declines were greater in oak than in beech, even though the photosynthetic rate of beech 388 was found to significantly decrease at low water potentials, while oaks maintained high rates of photosynthesis even under very low leaf water potentials and high air 389 390 temperatures (Raftoyannis and Radoglou 2002). 391 Our investigation revealed that NDVI response to climatic stress was related to an increase in the reflectance in both red and near infrared band. While the increase in the 392 393 red band can be related to the reduced rate of absorption of the photosyntheticaly active 394 radiation (Glenn et al. 2008), increased reflectance in the near infrared band currently 395 lacks an acceptable interpretation. This spectral range is mainly sensitive to internal leaf structure and leaf dry matter content (Ceccato et al. 2001), and is normally expected to increase with vegetation curing (drying and dying; Cheney and Sullivan 1997). However, in our verification experiment (Appendix C), the increase in the reflectance in the near infrared band was minor compared to that of the red band. Caccamo et al. (2011) stated that the evaluation of performance of MODIS-derived spectral indices in the visible, near infrared and short wave infrared bands has only been conducted in agricultural areas but not for high biomass ecosystems; therefore further research is needed to understand such responses thoroughly. The sensitivity analysis indicated that the two species respond to slightly different drivers of environmental stress. GDD, and mean and maximum daily temperatures above 20 and 24°C respectively, concurrent to rainless periods, were the most important variables in driving the observed declines in NDVI in beech stands. In temperate climate the probability of physiological drought is closely correlated with the period of greatest photosynthetic activity, the fact that GDD is the best predictor of NDVI decline in beech suggests a strong link to phenology with diminished potential for adaptation to the environmental stress driver. The strong link of observed stress episodes to GDD may thus imply that beech – in contrast to oak – may lack sufficient phenotypic plasticity to mitigate the effects of expected climate change. In this regard, Nahm et al. (2007) found uniform drought response of beech stands distributed from southern France to central Germany. Mátyás et al. (2010) suggest that phenotypic plasticity of beech populations is considerable, but ceases to buffer stress near the xeric limit of the species. On the other hand, Weber et al. (2013) suggested that beech near their dry distribution limit are adapted to extreme conditions already and should be less affected physiologically, while changes in the growth patterns of beech under mesic conditions have to be expected. Strong effect of GDD on beech stress response may be related to the functionality of antioxidant systems (Rennenberg et al. 2006). Polle et al. (2001) claim that under

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extended periods of drought and elevated air temperatures, mature beech leaves which were normally highly stress-tolerant became very susceptible to oxidative stress, what may be the case of our observations. The relationship between the length of drought periods and NDVI declines in our beech stands is linear, supporting the assertion of Leuzinger et al. (2005) that beech does not possess a coping mechanism which would limit the effect of cumulative damage. Nahm et al. (2007), however, argue in their investigation of beech performance after extreme heat and drought in summer 2003 that beech possess effective regulation mechanisms when facing even severe drought and heat periods. This issue does not appear to be settled yet, other authors found adverse effects of heat and drought on beech physiological performance (e.g. Epron and Dreyer 1993; Raftoyannis and Radoglou 2002; Wamelink et al. 2009), including effect on tree growth (Scharnweber et al. 2011). In contrast to beech, the magnitude of NDVI declines in oak stands was found to be sensitive primarily to increased temperature in a unimodal pattern. Our data show that increasing the number of days which exceed a temperature threshold and/or prolonging the rainless period does not have a linear effect on the decrease of NDVI. Species which evolved to colonise drier environments tend to cope better with episodes of drought accompanied by high temperatures than mesic-adapted species (Sack, 2004; Engelbrecht et al., 2005). A crucial difference in the physiology of beech and oak might explain the reduction of photosynthetic activity observed in this study in response to drought (Figure 3). Beech typically displays isohydric behaviour of progressively limiting stomatal conductance to maintain water potential (Cochard 1999), which is likely reflected in linearly decreasing rate of photosynthesis. Oaks, on the other hand, have been shown to use their extensive root systems to support anisohydric behaviour of tolerating decreasing water potential (Thomsen 2013). Stomata closure would initially limit

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transpiration as water availability decreases at the onset of drought, but do not close completely to maintain limited carbon fixation as the drought continues.

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4.2 Methodological comments and limitations

Daily observations of MODIS sensor with spatial resolution 250×250 meters can provide highly valuable data in many fields of vegetation science. There are, however, numerous obstacles which need to be overcome to gain reasonable confidence in the inferences based on such data. The substantial noise present in the data requires a comprehensive quality control to facilitate their use (Wang et al. 2003, Hmimina et al. 2013). The anisotropy in the spectral reflectance of vegetation has also been recognized as factor potentially limiting the use of daily NDVI data, and corrections to reduce this effect have been proposed (e.g. Shuai et al. 2013). While quality assurance metadata and other QA procedures can be used to substantially reduce the noise in daily data, effect of anisotropical reflectance persists. The use of 16-day MODIS products is suggested to avoid this effect, this product however does not offer the potential to study immediate vegetation responses to climatic and other stresses. The fact that we accepted an assumption of forest vegetation representing a Lambertian surface (i.e. with isotropic reflectance) should not significantly affect our analysis. Franch et al. (2013) found that while relative errors due to the Lambertian assumption in daily MODIS data are 3-12% in visible and 0.7-5% in infrared spectrum, they reach only 1% in NDVI. Indeed, this effect could have been further reduced by removing images taken under high zenith angles as was applied in this study. The aforementioned factors may indeed have affected the stress patterns observed in this study. We argue that such effects are random and cannot therefore generate a skewed pattern which could be interpreted as a continuous NDVI decline. In reality, this type of noise increases the variability in the data and potentially covers some less distinct stress patterns, thus contributing to the portion of variability which could not have been explained by the regression models developed in this study. To address this issue in greater detail, we conducted a supplementary investigation of the spectral response of drying oak leaves using laboratory hemispheric spectroradiometer. In spite of limited comparability of MODIS-based and laboratory-acquired spectral responses, our experiment generated response which was highly consistent with that of MODIS (see Appendix C for details). This finding supports our inferences and suggests that a deviation from Lambertian assumption should not prevent the daily MODIS NDVI data from being used in the research of diurnal vegetation dynamics. High performance of tested regression models implies strong control of climatic variables over the physiological response of beech and oak, leading to their potential use in predicting drought stress from meteorological observations and improving parameterisation of forest drought-stress indices. However, we identified a large number of rainless periods of various duration, which did not induce an observable stress response. Some are due to the inherent variability in tree response to moderate environmental stress driven by the phenotypic plasticity (Valladares et al. 2007) and environmental heterogeneity beyond the scale of observation. Others are generated by missing or discarded NDVI observations due to pixel contamination or other reasons. The use of rainless periods as indicators of drought stress in forest ecosystems has certain limitations due to varying soils characteristics and landscape topography, which both affect water availability to trees. In this study such effects were controlled for by considering relief and soils in the initial plot selection, however caution must be exercised when applying this methodology to a large or heterogeneous area. Precipitation measured with rain gauges can be used as highly reliable input data, vegetation vigour was repeatedly found very responsive to precipitation regime (e.g. Clifford et al. 2013; Plaut et al. 2013). Although not feasible in this study, meteorological indicators of drought should be verified and parameterised by direct measurements of soil water content for best reliability of stress prediction.

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The forest area covered in this study extends to ca. 20,000 km², however for the purpose of this study we identified only 121 MODIS pixels (250×250 m) which met the selection criteria. The spatial resolution of MODIS data was a factor severely limiting the number of suitable forest stands, chiefly due to our criterion of at least 99% cover of target species in each MODIS pixel, but also due to limits on stand exposition, elevation and soil type. Such strict selection, however, was applied for the purpose of inter-specific comparison of stress responses and may not be necessary for different goals, such as assessing stress status of large tracts of forests. The presented approach is suitable for tree species with continuous cover, rather than for species with scattered distribution or for open canopy situations.

5. Conclusion

Our analysis shows that MODIS-derived data describing intra-seasonal variation in NDVI values can indicate periods of environmental stress in beech and oak forests. We show that the incidence and magnitude of observed stress episodes can be explained by a set of environmental variables describing temperature and precipitation patterns. Having dissected the sensitivity of outlined methodology, we argue that MODIS data can be used to infer and verify interactions between climate and forest vigour and productivity in temperate broadleaf species with continuous distribution. In addition, a close examination of stand-specific time series of MODIS-NDVI can provide ecophysiological data complementary to terrestrial forest monitoring.

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 $\textbf{Table 1} \ \text{Criteria for the selection of forest stands used for the assessment of heat and drought effect on beech and oak stands}$

Limits
>99%
<670 m a.s.l. for oak; <850 m a.s.l. for beech
southern slopes
>50 years
<15 km from station with air temperature data;
< 7 km from station with precipitation data
Single-storey stands only
Homogenous across the pixels within group

Table 2 Descriptive data of beech and oak forest stands covered by the clusters of MODIS pixels used in the investigation NDVI response to drought and heat stress. Mean values and standard deviations are given.

-	EP	NoP	Altitude	Slope	Aspect	Age	Density	DifAltT	DifAltP	DifT	DifP
			[m a.s.l.]	[%]	[°]	[years]	[-]	[m a.s.l.]	[m a.s.l.]	[m]	[m]
	1	6	479±26	13±3.8	235±8	62±13	0.9±0.1	484	226	5,247	2,681
	2	4	515±25	16±2.8	189±18	97±41	0.8±0.1	533	533	5,182	5,186
	3	4	526±17	9±1.3	159±28	95±18	0.8±0.1	533	533	4,397	4,401
	4	5	433±34	10±2.7	148±32	113±7	0.8±0.1	533	225	11,812	5,625
BEECH EXPERIMENTAL PLOTS	5	4	655±72	29±2.6	150±36	121±9	0.6±0.1	254	315	9,177	3,331
ENTAL	6	4	688±63	31±3.2	192±38	139±3	0.7±0.0	254	650	11,047	2,585
CPERIM	7	7	714±68	29±1.8	174±62	103±6	0.8±0.0	411	502	7,902	3,283
ЕСН ЕХ	8	5	742±106	26±4.3	138±19	114±7	0.7±0.0	875	583	5,535	4,620
BE	9	4	686±22	11±1.2	237±8	88±6	0.8±0.1	140	397	14,481	2,906
	10	10	491±26	13±1.8	212±27	97±10	0.7±0.1	305	287	5,792	5,263
	11	4	443±31	16±1.6	239±14	92±5	0.7±0.0	305	262	6,216	3,305
	12	2	398±21	17±1.5	126±13	100±0	0.7±0.0	305	232	16,275	6,633
	13	7	505±24	14±1.3	196±55	78±6	0.8±0.0	122	338	12,631	2,566
	1	10	397±31	11±2.6	170±16	93±13	0.8±0.1	180	315	13,564	4,806
	2	5	410±28	13±2.0	225±0	98±13	0.7±0.1	318	191	10,406	5,066
LOTS+	3	4	544±8	6±3.6	201±36	54±2	0.9±0.1	139	241	13,290	5,987
NTAL P	4	10	574±57	15±2.4	176±41	83±17	0.7±0.0	318	338	2,676	2,241
OAK EXPERIMENTAL PLOTS+	5	7	186±7	2±0.4	141±16	71±13	0.7±0.0	110	117	8,550	6,878
	6	6	376±24	8±1.8	176±63	85±1	0.8±0.0	100	160	9,005	2,923
	7	6	295±22	11±1.2	78±23	75±15	0.8±0.0	100	160	7,475	3,925
	8	7	174±4	3±1.7	92±107	67±9	0.7±0.0	100	100	7,116	1,916

Abbreviations: EP – Experimental Plot; NoP – Number of MODIS Pixels covering an EP; Slope – mean relief slope within an EP; Aspect – mean relief aspect within an EP; Density – mean stand density within an EP; DiffAltT – mean altitudinal difference between an EP and meteorological stations used for the air temperature interpolation; DifAltP – altitudinal difference between an EP and the meteorological station used for the calculation of rainless periods; DiftT – mean horizontal distance between an EP and meteorological stations used for the calculation of rainless periods

Table 3 Descriptive statistics of maximum observed NDVI declines, described in terms of percentage decline from the total NDVI amplitude, that occurred as a result of potential drought and heat stress during the period 2000–2010 in oak and beech stands in Central Europe. The variable describes the maximum stress induced by climatic factors to beech and oak that was recorded using MODIS imagery.

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	N	Mean	Med	Min	Max	0.25	0.75	StDev
Beech	166.00	10.59	8.88	5.00	27.55	6.59	12.74	691
Oak	173.00	12.47	9.71	5.00	41.81	6.86	14.53	8.70 692

Table 4 Descriptive statistics of explanatory variables used in the regression modelling of drought and heat effects on the variation in MODIS NDVI in oak and beech stands in Central Europe

	BEECH EXPERIMENTAL PLOTS									OAK EXPERIMENTAL PLOTS						
Variables	N	Mean	Med	Min	Max	StDev	N	Mean	Med	Min	Max	StDev				
GDD	167	767	703	349	1443	332	173	917	954	334	1410	334				
Tavg	167	19.37	18.90	13.50	24.20	2.56	173	19.39	19.30	15.90	23.20	1.84				
Tmax	167	31.57	32.10	27.40	35.20	2.33	173	31.35	31.70	26.60	35.00	2.24				
Tmin	167	8.25	8.60	-0.50	15.90	4.55	173	8.43	8.60	3.60	13.10	2.71				
N-Tavg >15°C	167	10.59	9.00	4.00	27.00	4.97	173	12.31	11.00	4.00	42.00	5.57				
N-Tavg >18°C	167	8.10	7.00	2.00	18.00	4.02	173	9.52	9.00	2.00	32.00	4.93				
N-Tavg >21°C	167	4.62	5.00	0.00	13.00	3.93	173	4.62	4.00	0.00	14.00	2.94				
N-Tavg >24°C	167	1.80	1.00	0.00	6.00	2.10	173	1.24	1.00	0.00	8.00	1.53				
N-Tavg >27°C	167	0.08	0.00	0.00	1.00	0.28	173	0.00	0.00	0.00	0.00	0.00				
N-Tmax >20°C	167	11.49	10.00	5.00	29.00	5.24	173	12.98	11.00	5.00	42.00	5.30				
N-Tmax >23°C	167	9.41	8.00	4.00	22.00	3.97	173	11.29	10.00	4.00	38.00	5.16				
N-Tmax >26°C	167	7.32	7.00	3.00	13.00	2.97	173	7.55	7.00	1.00	26.00	3.88				
N-Tmax >29°C	167	3.96	5.00	0.00	10.00	3.08	173	3.76	4.00	0.00	12.00	2.98				
N-Tmax >32°C	167	1.19	1.00	0.00	4.00	1.43	173	1.04	0.00	0.00	6.00	1.48				
N-Tmax >35°C	167	0.06	0.00	0.00	1.00	0.24	173	0.00	0.00	0.00	0.00	0.00				
Drt	166	13	10.00	5.00	27.00	5.99	173	13	12.00	5.00	24.00	5.19				
Age	167	89	91	50	135	17	173	77	81	50	112	12				
Elev	167	531	500	391	845	105	173	341	320	166	661	134				

Abbreviations: GDD –growing degree days; Drt – length of drought period; Age – mean stand age; Elev – mean stand elevation; Tavg – mean air temperature during a drought period; Tmin – minimum air temperature during a drought period; N-Tavg >18°C (or >21°C, >24°C, >27°C) – number of days with mean air temperature above 18° C (or above 21° C, 24° C, 27° C), which occurred during a stress episode; N-Tmax >20°C (or >23°C, >26°C, >29°C, >32°C, >35°C) – number of days with maximum air temperature above 20° C (or above 23° C, 26° C,

Table 5 Mean Pearson's correlation coefficients between Neural Networks predicted and observed decline in NDVI value of beech and oak stands calculated for training, testing and validation sets. These coefficients are calculated from a set of the best performing Neural Networks. Correlation coefficients indicate the overall performance of neural network-based regression models

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	Training	Testing	Validation
Beech	$0.86 \pm 6\%$	$0.82 \pm 8\%$	$0.93 \pm 0.6\%$
Oak	$0.88 \pm 1.0\%$	$0.81 \pm 9\%$	$0.96\pm0.3\%$

Table 6 Mean sensitivity scores of explanatory variables produced by 15 best-performing Neural Networks. The scores indicate the predictive power of explanatory variables in explaining the observed declines in NDVI values induced by heat and drought stress. The higher the score, the closer the relationship between the explanatory and the dependent variables.

BEECH I	BEECH EXPERIMENTAL PLOTS																
GDD	N-Tmax	N-Tmax	Tmax	N-Tavg	N-Tavg	Tmin	N-Tmax	N-Tavg	N-Tavg	Tavg	Age	N-Tmax	N-Tmax	Drt	Elev	Slope	Aspect
	>29°C	>20°C		>24°C	>18°C		>32°C	>21°C	>15°C			>26°C	>23°C				
4.62	4.00	3.90	3.31	3.29	2.68	2.51	2.42	2.34	2.31	1.50	1.50	1.43	1.28	1.27	1.19	1.13	1.04
OAK EX	PERIMEN	TAL PLOT	ΓS														
N-Tavg	N-Tmax	N-Tmax	N-Tavg	GDD	N-Tmax	Tmax	N-Tavg	Tavg	Age	Tmin	Drt	Elev	N-Tavg	N-Tmax	Aspect	Slope	N-Tmax
>24°C	>32°C	>29°C	>21°C		>20°C		>15°C						>18°C	>26°C			>23°C
5.60	3.18	2.51	1.63	1.61	1.54	1.54	1.53	1.48	1.42	1.38	1.32	1.29	1.28	1.24	1.23	1.18	1.17

Abbreviations: GDD – growing degree days; Drt – length of drought period; Age – mean stand age; Elev – mean stand elevation; Tavg – mean air temperature during a drought period; Tmax – maximum air temperature during a drought period; Tmax – maximum air temperature during a drought period; N-Tavg >18°C (or >21°C, >24°C, >27°C) – number of days with mean air temperature above 21°C, 24°C, 27°C), which occurred during a stress episode; N-Tmax >20°C (or >23°C, >26°C, >29°C, >32°C, >35°C) – number of days with maximum air temperature above 20°C (or above 23°C, 26°C, 29°C, 32°C, 35°C), which occurred during a stress episode

724 Figure captions 725 Fig. 1 Position of the clusters of MODIS pixels covering homogenous mature beech and oak stands 726 used for the investigations of MODIS-NDVI response to drought and heat stress. Meteorological 727 stations used for the interpolation of climate data to the position of analysed groups of pixels are also 728 shown. 729 Fig. 2 Seasonal course of MODIS-NDVI observations from a single stand in one year (dots). Arrow 730 identifies a typical episode of NDVI decline symptomatic of climatic stress. NDVI_{max} represents the 731 mean of 2-4 NDVI observation immediately preceding a stress episode (local maximum), NDVI_{stress} is 732 the value at the end of a stress episode, and NDVI_{min} is the lowest NDVI value observed in local 733 734 conditions. 735 Fig. 3 Univariate relationships between maximum NDVI declines and predictor variables which were 736 identified as the most influential by neural networks-based regression modelling in oak stands. 737 738 739 Fig. 4 Univariate relationships between maximum NDVI declines and predictor variables which were 740 identified as the most influential by neural networks-based regression modelling in beech stands. 741 742 Fig. 5 Frequency of rainless periods longer than 3 days which did (dark columns) and did not (hashed 743 columns) induce an observable decline in NDVI 744

745 **Appendix captions** 746 Appendix A Example of experimental plots used for the investigation of MODIS-NDVI responses to climatic 747 748 stress. Each experimental plot in our experimental design consists of 4-13 MODIS pixels (250×250m) 749 750 Appendix B An example of declining sequences of MODIS-NDVI identified in NDVI time series for selected 751 752 beech and oak dominated MODIS pixels for the period 2000-2010. Such sequences are indicative of 753 environmental stress affecting the physiological performance and spectral reflectance of vegetation. 754

Appendix C

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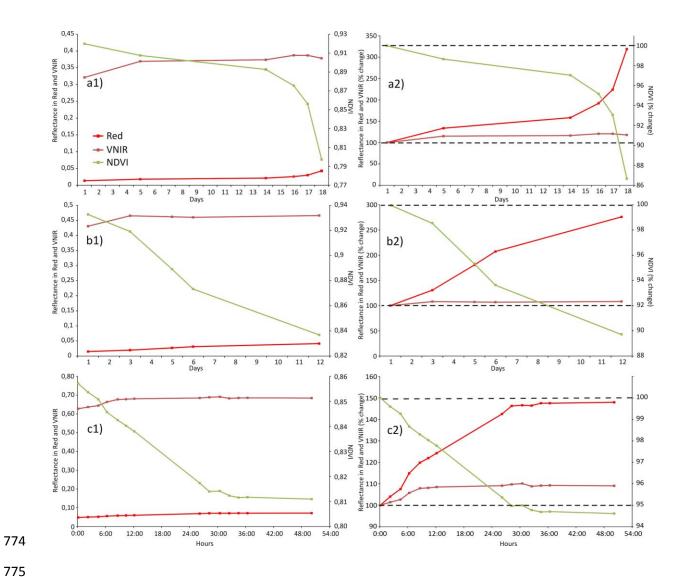
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Reflectance of mature homogenous stands within two MODIS pixels with spatial resolution 250×250 meters in red and near infrared (VNIR) spectral bands is shown in panes A) and B). Pane A) represents an 80 year old pure oak stand undergoing a rainless period lasting 18 days, while pane B) shows values from a pixel covering an 80 year old pure beech stand affected by a 12 day rainless period. Panes A1) and B1) show raw reflectance values, while A2) and B2) show percentage change relative to the reflectance measured on the day of the last rain event. Spectral reflectance values in panes C) were measured by the LI-1800 Portable Spectroradiometer using 1800-12 Integration Sphere (Licor Inc.) collecting radiation reflected from the sampled material illuminated by a glass-halogen lamp. Three fresh overlapping leaves of *Quercus* robur were positioned in the sphere chamber without water and continuous reflectance readings were recorded for 54 hours with unequal time step in the range 400-1100 nm. At the end of the observation, the leaves were dry beyond natural range found in the field conditions in Central Europe. This supplementary analysis shows that spectral change in leaves with limited water availability observed by the MODIS sensor at stand scale is very consistent with changes observed in laboratory conditions at the leaf scale. The latter is free of any atmospheric or weather related interferences. This indicates that, despite the limited comparability of the two sets of spectral responses, daily MODIS data can provide realistic information on vegetation stress dynamics which can be readily distinguished from intra-seasonal vegetation dynamics.



780 Figures

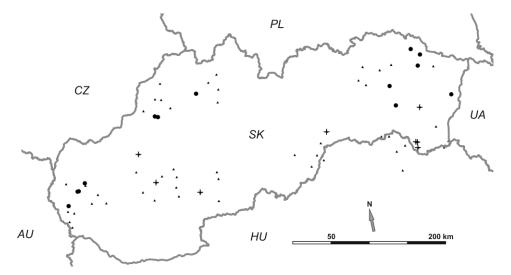


Fig. 1

