

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

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1	MODIS-based vegetation index has sufficient sensitivity to
2	indicate stand-level intra-seasonal climatic stress in oak and beech
3	forests
4 5	^{1,2} Tomáš Hlásny, ^{1,2} Ivan Barka, ¹ Zuzana Sitková, ¹ Milan Konôpka, ¹ Tomáš Bucha, ³ Martin Lukáč
6 7 8 9	¹ National Forest Centre – Forest Research Institute Zvolen, T. G. Masaryka 22, 960 92 Zvolen, Slovak Republic
10 11 12	² Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, 165 21 Prague 6, Czech Republic
13 14 15	³ School of Agriculture, Policy and Development, University of Reading, RG6 6AR, United Kingdom
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
- 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
- 42

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.

48 Introduction

49 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; 50 Leuzinger et al. 2005). Survival of woody species within their present range is likely to 51 52 be constrained by water availability, prolonged drought during vegetation season may 53 induce episodes of large-scale tree decline (Allen et al. 2010; McDowel et al. 2011). 54 Drought induced tree mortality has mainly been observed in the Mediterranean region, 55 affecting a range of species (for an overview see Allen et al. 2010). Further north, lack of 56 water has been identified chiefly as a predisposing factor for biotic stressors, for example 57 drought periods repeatedly triggering large-scale pest outbreaks (Rouault at al. 2006). In 58 temperate forests, repeated episodes of drought usually cause a decrease in leaf area index 59 (Le Dantec et al. 2000), often resulting in a decline in forest productivity (Glenn et al. 60 2008, Hlásny et al. 2011a). However, some recent observations such as drought induced 61 mass beech mortality (Lakatos and Molnár 2010) or drought-triggered pest outbreaks 62 (Mátyás et al. 2010) indicate the importance of drought as an emerging primary mortality 63 agent in temperate Europe. This link is underlined by the presence of drought sensitive 64 xeric limit of several temperate tree species, as well as by projections indicating drought 65 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 66 they constitute some of the ecologically and economically most important species. Oaks 67 are favoured by a relatively warm and dry climates (Czúcz et al. 2011; Epron and Dreyer 68 69 1993), while beech has been identified as sensitive to drought and potentially vulnerable 70 to climate change (Geßler et al. 2007; Mátyás et al. 2010; Leuzinger et al. 2005). Since 71 climate change may force a replacement of beech by oaks in some localities, the 72 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 active radiation by living plant foliage (Myneni and Williams 1994). Since photosynthetic 91 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 severity of vegetation stress resulting from a potential water deficit and excessive 95 96 temperatures in mature beech and oak stands in Central Europe. We hypothesize that (i) specific stress episodes can be identified in time series of MODIS-NDVI localised to 97

98	forest stands, and (ii) these patterns are linked to specific intensity and duration of
99	rainless and heat periods. We perform a regression modelling analysis to assess the
100	usefulness of MODIS imagery for investigations of intra-seasonal variation of forest
101	vigour and to identify environmental variables which best predict the stress response of
102	beech and oak stands.
103	
104	1. Materials and methods
105	2.1 Study region and experimental plots
106	The research focuses on the territory of Slovakia (Central Europe) where a number of
107	forest plots distributed across the whole country were identified. Forest management
108	plans and other databases archived by the National Forest Centre, Slovakia, were used to
109	localise experimental plots using criteria listed in Table 1.
110	Table 1
111	The purpose of stand selection was to create a database of mature and homogenous oak
112	and beech stands seamlessly covering groups of MODIS pixels (250×250 m, see
113	Appendix A). Oak stands contained mixtures of Sessile oak (Quercus petrea),
114	Pedunculate oak (Quercus robur) and Pubescent oak (Quercus pubescens). Only single-
115	layer stands with closed canopy were considered for this study. Each selected stand was
116	composed of at least 99% of the target species. This threshold was set arbitrarily high to
117	allow for a reasonable confidence in inter-specific comparison. To reduce the variability

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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 ex	perimental	plots covered by	v a total of	66 MODIS	pixels.	and 8 oal

123 plots covered by 55 MODIS pixels met the selection criteria (Fig. 1, Table 2).

124 Fig. 1

- **125** Table 2
- 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:
- 132

133 NDVI =
$$(\rho NIR - \rho Red)/(\rho NIR + \rho Red)$$
 Eq. 1

134

135 where ρ NIR and ρ Red are reflectance values of near infrared and red radiation.

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

the period 2000–2010 were derived from MODIS product MOD09GQ (Source: NASA

140 LP DAAC). Despite potentially adverse effect of anisotropical reflectance of vegetation

141 on the use of daily MODIS data (e.g. Shuai et al. 2013), we made preference for this

142 product over 16-day products with 500 m resolution which are free of this potentioal

- 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
- 145 critically limit the usability of such imagery. Indeed, Franch et al. (2013) suggested that

errors due to the Lambertian assumption in daily MODIS data are likely to be negligiblein case of NDVI values.

148 Since clouds and atmospheric aerosols can introduce substantial noise in MODIS NDVI 149 data (Wang et al. 2003, Hmimina et al. 2013), a two-step quality control has been applied 150 to remove observations contaminated by atmospheric or other interference. First, 151 MOD09GA (500x500) product was used to exclude images taken under high sensor 152 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 153 154 latter product does not contain information on pixel contamination by aerosols. 155 Moreover, MOD09GA contains information detected in all spectral bands of MODIS (range 459–2,155 nm), supporting its superior performance in the detection of 156 157 contaminated pixels. Indeed, cloud masks based on this product have been shown to 158 slightly overestimate real clouding (Kotarba et al. 2009). Despite a very conservative first 159 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 160 161 manual quality control procedure aimed at removal of NDVI values which were 162 inconsistent with the expected annual cycle of vegetation greenness (Bruce et al. 2006). 163

164 2.3 Climate data and definition of drought and heat periods

165 Daily meteorological data collected at 46 meteorological stations in the vicinity of

166 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

- 169 of conditions specific to each experimental plot were selected from the national network
- 170 of stations using the following criteria: horizontal and vertical distance from selected

stands (Table 1); landscape orography and climatic variability of broader surroundings.

172 The latter two criteria were included to prevent interpolation over mountain ridges and

across climatically different regions.

174 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

177 recorded per day. This value represents precipitation with low probability of reaching the

178 roots due to interception loss in the canopy (van de Salm et al. 2007), as well as

179 evaporation from the ground. Since no information on actual soil or leaf water content is

180 available at the desired scale and terrain cover, we use the duration of rainless periods as

181 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 suchinterpretation.

184 A heat period was defined as sequence of days with mean or maximum air temperature

185 exceeding arbitrarily set thresholds (Table 4).

186 2.4 Identification of stress episodes in MODIS-NDVI time series 2000-2010

187 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

189 expressed in terms of actual decline in NDVI relative to the overall permissible decline

- 190 observed in each MODIS pixel (local amplitude) and calculated according to the
- 191 following formula:
- 192

193
$$NDVI_{decline} = 100 - ((NDVI_{max} - NDVI_{stress})/(NDVI_{max} - NDVI_{min}) \times 100)$$
 Eq. 2

195	where $NDVI_{max}$ represents the NDVI of unstressed vegetation and is calculated as the
196	mean of 2-4 NDVI observations immediately preceding a stress episode, $NDVI_{stress}$ is a
197	value in a sequence of declining NDVI values, and NDVI_{min} is the lowest value of annual
198	NDVI amplitude, correspondent with a period without foliage. $NDVI_{min}$ was constant
199	during the investigated 10 year period, reaching 0.52 for beech and 0.44 for oak; these
200	values were found to be uniform across all investigated plots and in all years. The
201	difference between $NDVI_{max}$ and $NDVI_{min}$ defines the local amplitude for each pixel (Fig.
202	2). Introducing local amplitudes allows for comparability of NDVI declines in spite of
203	inter-annual and inter-pixel variability in $NDVI_{max}$. In addition, $NDVI_{max}$ of unstressed
204	vegetation constantly declines from spring to late summer, i.e. from ca. 1.0 to 0.9
205	(Soudani et al. 2012); hence the need for data standardisation. As a consequence, the local
206	amplitude of NDVI is smaller in beech (0.52 to local maximum) than in oak (0.44 to local
207	maximum).
208	Only stress episodes consisting of at least 3 sequentially declining values observed in at
209	least two MODIS pixels from each experimental plot were considered. Also, the
210	magnitude of each decline was set to exceed 5% of local NDVI amplitude. Stress
211	episodes were extracted manually for each pixel during the vegetative season over the
212	entire 10-year period. The length and timing of periods of full foliage differed between
213	years and pixels, as indicated by the seasonal course of NDVI values. The fact that only
214	the period of full foliage was considered, together with the strict stand selection criteria
215	described earlier, implies that forest understory and herbaceous layer should not affect the
216	evaluated spectral response.
217	

218 Fig. 2

220 2.5 Regression modelling of observed stress episodes and climate

221 Three types of interaction between stress episodes and climatic extremes may occur in 222 this type of studies; (i) climate extremes (rainless and/or heat periods) correspond with 223 incidence of NDVI declines (True Responses, TRs), (ii) NDVI declines occur in periods 224 when no heat and rainless period has occurred (False Responses, FRs), (iii) no NDVI 225 decline is apparent during heat and rainless periods (False Triggers, FTs). An inclusion of 226 FRs and FTs in the regression analysis is not possible because either the dependent or 227 explanatory variable(s) would be missing. However, a very high occurrence of FRs and 228 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. 229 230 Maximum NDVI_{decline} value observed in each stress episode (Eq. 2, Fig. 2) is used as the 231 dependent variable and regressed against the list of explanatory variables given in Table 232 4. Regression modelling was run independently for the two species to facilitate an 233 evaluation of inter-specific differences in stress response. First, bootstrap sampling was 234 applied repeatedly to randomly split input data into training, testing, and validation sets in 235 the ratio of 70:15:15. Then, Neural Network-based modelling was used, following the 236 workflow described by Hlásny et al. (2011b). In total, 2,000 Neural Networks with 237 varying architecture were trained for each species; the training represents an iterative 238 fitting of a neural network-based model into parameterisation data while controlled by testing and validation samples. Correlation coefficients between NDVI_{decline} values 239 240 predicted by trained Neural Networks and observations allocated to testing and validation 241 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 242 coefficients between observed and predicted NDVIdecline values) out of the initial set of 243

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

246 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

248 produced by a Neural Network with a missing variable relative to the error of a Network

249 with the full set of input variables. The more sensitive the network is to the inclusion of a

250 particular input, the greater the measured deterioration of prediction and therefore the

251 greater the error ratio (1 represents a neutral relationship).

252 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

256 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

258 Statistica Neural Networks v.10 (StatSoft Inc., 2004).

259 260

2. Results

261 **3.1 Stress episodes**

262 The mean length of observed continuous declines in NDVI was 10.6 days in beech and

263 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).

265 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

267 NDVI_{decline} was larger in oak stands; standard deviation of declines reached 57% of mean

268 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

270 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

272 observable decline in NDVI values. Stress episodes always ended at first precipitation

event which cancelled the respective rainless period. NDVI recovered to its local

274 maximum shortly after and no irreversible changes were observed.

275 Table 3

276 As a technical verification study, we explored spectral responses of foliage to drought in 277 the red (620-670 nm) and near infrared band (840-876 nm, Appendix C). The same bands 278 were used to calculate NDVI values in the main objective of this manuscript (Eq. 1). 279 Bench-top NDVI declines are mainly related to an increased reflectance in the red band, 280 which is indicative of reduced photosynthetic performance of vegetation (i.e. lesser absorption and higher reflectance of photosyntheticaly active radiation, Reflectance in the 281 282 near infrared band was found to increase as well, although the pattern of increase was not 283 as clear as that of the red band. We observed more than threefold increase in the 284 reflectance in the red band at the end of stress periods lasting from 10 to 20 days, as 285 compared to unstressed vegetation. Increased absorption in the near infrared band, which 286 could be indicative of drought induced changes in leave cell walls, was not observed in 287 the current investigation. 288

289 **3.2 Regression modelling**

290 Correlations between predicted and observed values, calculated as the mean of 15 best

291 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

293 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.

296 Table 5

297 Sensitivity scores (SS) produced by the 15 best-performing regression models were found 298 to be highly consistent among the models. PC1 explained 81% of the total variability of 299 SS in beech and 76% in oaks and SS of no model differed significantly from the main 300 pattern represented by PC1. Differences in mean sensitivity scores indicated variation in the predictive power of explanatory variables between the two tree species, suggesting 301 302 diverging physiological capacity to respond to heat and drought stress (Table 6). The 303 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 304 days with average air temperature above 24°C was the most influential variable in oak 305 306 (SS=5.60), whilst in beech the number of days with maximum air temperature above 29 307 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 308 (15th order with SS=1.27 in beech, and 12th order with SS=1.32 in oak), and its 309 310 importance was greatly subdued by heat-related variables. Non-climatic variables such as 311 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 312 313 significantly from each other, as well as from all lower-rank variables (α =0.05, Tab. 6). In 314 beech, the decrease in SS from the first to the last-ranked variable was not so apparent, 315 however the mean SS of the group of most influential variables was significantly 316 different from the lower-rank variables. Table 6 317

320 **3.3 Univariate responses**

321 In order to understand the phenological and physiological implications of the most 322 influential explanatory variables, we further analysed dominant relationships. Diverging 323 response to the most influential climatic variables was found in oak, which has shown 324 highest NDVI declines at short to medium duration of unfavourable climate, while longer 325 duration stress events were accompanied by less severe NDVI declines. The largest 326 decreases of NDVI were induced by 1-2 hot days accumulated during stress episodes 327 with average daily air temperature above 24° C (the most influential variable, SS=5.60), 328 though the variability of responses was high (Fig. 3a). Unimodal response was observed 329 at N-Tmax>29°C (SS=2.51) with maximum NDVI declines at around 2-4 days (Fig. 3b). 330 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 331 332 above 32° C); the reason for this is the low number of stress episodes during which days 333 with air temperature exceeded the threshold of 32°C. 334 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

337 between the most influential climatic variables and the stress response of beech are

338 presented in Fig. 4.

339 Fig. 4

340 The only explanatory variable to which we observed a unimodal response in both species

341 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

345	precipitation event and NDVI recovers to its local and seasonal maximum shortly after.
346	Considering it on a univariate basis indicates a linear relationship between the length of
347	drought and corresponding magnitude of NDVI declines in beech, but a quadratic
348	relationship in oak (Fig. 3d, 4d).
349	

350 3.4 Incidence of False Responses and False Triggers

351 Relationships between frequencies of rainless periods longer than 4 days which were

352 characterised by at least 3 non-declining NDVI observations and rainless periods

353 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

355 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

357 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

359 substantially higher than the frequency of rainless periods inducing stress response for all

360 durations of rainless periods.

361 Fig. 5

362

363 3. Discussion

364 4.1 Ecophysiological inference and applicability

365 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

367 competitive advantage under projected climatic changes (Scharnweber et al. 2011).

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

has been identified (Epron and Dreyer 1993; Raftoyannis and Radoglou 2002; Wamelinket al. 2009).

372 As indicated in our analysis, drought approximated by the duration of rainless periods

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

NDVI time series. Generally, drought-induced damage may lead to organ dysfunction,

377 but it only seldom results in direct and immediate induction of tree decline and death

378 (Bréda et al. 2006). Hence, continuous decline of NDVI values in years following

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

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

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

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

389 rates of photosynthesis even under very low leaf water potentials and high air

temperatures (Raftoyannis and Radoglou 2002).

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 red band can be related to the reduced rate of absorption of the photosynthetically active radiation (Glenn et al. 2008), increased reflectance in the near infrared band currently lacks an acceptable interpretation. This spectral range is mainly sensitive to internal leaf 396 structure and leaf dry matter content (Ceccato et al. 2001), and is normally expected to 397 increase with vegetation curing (drying and dying; Cheney and Sullivan 1997). However, 398 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 399 400 that the evaluation of performance of MODIS-derived spectral indices in the visible, near 401 infrared and short wave infrared bands has only been conducted in agricultural areas but 402 not for high biomass ecosystems; therefore further research is needed to understand such 403 responses thoroughly.

404 The sensitivity analysis indicated that the two species respond to slightly different drivers 405 of environmental stress. GDD, and mean and maximum daily temperatures above 20 and 406 24°C respectively, concurrent to rainless periods, were the most important variables in 407 driving the observed declines in NDVI in beech stands. In temperate climate the 408 probability of physiological drought is closely correlated with the period of greatest 409 photosynthetic activity, the fact that GDD is the best predictor of NDVI decline in beech 410 suggests a strong link to phenology with diminished potential for adaptation to the 411 environmental stress driver. The strong link of observed stress episodes to GDD may thus 412 imply that beech - in contrast to oak - may lack sufficient phenotypic plasticity to 413 mitigate the effects of expected climate change. In this regard, Nahm et al. (2007) found 414 uniform drought response of beech stands distributed from southern France to central 415 Germany. Mátyás et al. (2010) suggest that phenotypic plasticity of beech populations is 416 considerable, but ceases to buffer stress near the xeric limit of the species. On the other 417 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 418 419 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 420 421 antioxidant systems (Rennenberg et al. 2006). Polle et al. (2001) claim that under

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.

425 The relationship between the length of drought periods and NDVI declines in our beech 426 stands is linear, supporting the assertion of Leuzinger et al. (2005) that beech does not 427 possess a coping mechanism which would limit the effect of cumulative damage. Nahm 428 et al. (2007), however, argue in their investigation of beech performance after extreme 429 heat and drought in summer 2003 that beech possess effective regulation mechanisms 430 when facing even severe drought and heat periods. This issue does not appear to be 431 settled yet, other authors found adverse effects of heat and drought on beech 432 physiological performance (e.g. Epron and Dreyer 1993; Raftoyannis and Radoglou 433 2002; Wamelink et al. 2009), including effect on tree growth (Scharnweber et al. 2011). 434 In contrast to beech, the magnitude of NDVI declines in oak stands was found to be 435 sensitive primarily to increased temperature in a unimodal pattern. Our data show that 436 increasing the number of days which exceed a temperature threshold and/or prolonging 437 the rainless period does not have a linear effect on the decrease of NDVI. Species which 438 evolved to colonise drier environments tend to cope better with episodes of drought 439 accompanied by high temperatures than mesic-adapted species (Sack, 2004; Engelbrecht et al., 2005). A crucial difference in the physiology of beech and oak 440 441 might explain the reduction of photosynthetic activity observed in this study in response 442 to drought (Figure 3). Beech typically displays isohydric behaviour of progressively 443 limiting stomatal conductance to maintain water potential (Cochard 1999), which is likely 444 reflected in linearly decreasing rate of photosynthesis. Oaks, on the other hand, have been 445 shown to use their extensive root systems to support anisohydric behaviour of tolerating 446 decreasing water potential (Thomsen 2013). Stomata closure would initially limit

447 transpiration as water availability decreases at the onset of drought, but do not close

448 completely to maintain limited carbon fixation as the drought continues.

449

450 **4.2 Methodological comments and limitations**

Daily observations of MODIS sensor with spatial resolution 250×250 meters can provide 451 452 highly valuable data in many fields of vegetation science. There are, however, numerous 453 obstacles which need to be overcome to gain reasonable confidence in the inferences 454 based on such data. The substantial noise present in the data requires a comprehensive 455 quality control to facilitate their use (Wang et al. 2003, Hmimina et al. 2013). The 456 anisotropy in the spectral reflectance of vegetation has also been recognized as factor 457 potentially limiting the use of daily NDVI data, and corrections to reduce this effect have 458 been proposed (e.g. Shuai et al. 2013). While quality assurance metadata and other QA 459 procedures can be used to substantially reduce the noise in daily data, effect of 460 anisotropical reflectance persists. The use of 16-day MODIS products is suggested to 461 avoid this effect, this product however does not offer the potential to study immediate 462 vegetation responses to climatic and other stresses. The fact that we accepted an 463 assumption of forest vegetation representing a Lambertian surface (i.e. with isotropic 464 reflectance) should not significantly affect our analysis. Franch et al. (2013) found that 465 while relative errors due to the Lambertian assumption in daily MODIS data are 3-12% in 466 visible and 0.7-5% in infrared spectrum, they reach only 1% in NDVI. Indeed, this effect 467 could have been further reduced by removing images taken under high zenith angles as 468 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 474 explained by the regression models developed in this study. To address this issue in 475 greater detail, we conducted a supplementary investigation of the spectral response of 476 drying oak leaves using laboratory hemispheric spectroradiometer. In spite of limited comparability of MODIS-based and laboratory-acquired spectral responses, our 477 478 experiment generated response which was highly consistent with that of MODIS (see 479 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 480 481 from being used in the research of diurnal vegetation dynamics.

482 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 483 484 predicting drought stress from meteorological observations and improving 485 parameterisation of forest drought-stress indices. However, we identified a large number 486 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 487 488 environmental stress driven by the phenotypic plasticity (Valladares et al. 2007) and 489 environmental heterogeneity beyond the scale of observation. Others are generated by 490 missing or discarded NDVI observations due to pixel contamination or other reasons.

491 The use of rainless periods as indicators of drought stress in forest ecosystems has certain

492 limitations due to varying soils characteristics and landscape topography, which both

493 affect water availability to trees. In this study such effects were controlled for by

494 considering relief and soils in the initial plot selection, however caution must be exercised

495 when applying this methodology to a large or heterogeneous area. Precipitation measured

496 with rain gauges can be used as highly reliable input data, vegetation vigour was

497 repeatedly found very responsive to precipitation regime (e.g. Clifford et al. 2013; Plaut

498 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

500 best reliability of stress prediction.

The forest area covered in this study extends to ca. 20,000 km², however for the purpose 501 502 of this study we identified only 121 MODIS pixels (250×250 m) which met the selection 503 criteria. The spatial resolution of MODIS data was a factor severely limiting the number 504 of suitable forest stands, chiefly due to our criterion of at least 99% cover of target 505 species in each MODIS pixel, but also due to limits on stand exposition, elevation and 506 soil type. Such strict selection, however, was applied for the purpose of inter-specific 507 comparison of stress responses and may not be necessary for different goals, such as 508 assessing stress status of large tracts of forests. The presented approach is suitable for tree 509 species with continuous cover, rather than for species with scattered distribution or for 510 open canopy situations.

511 512

5. Conclusion

513 Our analysis shows that MODIS-derived data describing intra-seasonal variation in NDVI 514 values can indicate periods of environmental stress in beech and oak forests. We show 515 that the incidence and magnitude of observed stress episodes can be explained by a set of 516 environmental variables describing temperature and precipitation patterns. Having 517 dissected the sensitivity of outlined methodology, we argue that MODIS data can be used 518 to infer and verify interactions between climate and forest vigour and productivity in 519 temperate broadleaf species with continuous distribution. In addition, a close examination 520 of stand-specific time series of MODIS-NDVI can provide ecophysiological data 521 complementary to terrestrial forest monitoring.

522

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531 **References**

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M,
- 533 Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z,
- 534 Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A
- 535 global overview of drought and heat-induced tree mortality reveals emerging climate
- change risks for forests. For Ecol Manage 259:660–684.
- 537 Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under
- severe drought: a review of ecophysiological responses, adaptation processes and long-
- term consequences. Ann For Sci 63:625–64.
- 540 Bruce LM, Mathur A, Byrd JD Jr. (2006) Denoising and Wavelet-Based Feature
- 541 Extraction of MODIS Multi-Temporal Vegetation Signatures. GIScience & Remote
- 542 Sensing 43:67–77.
- 543 Caccamo G, Chisholm LA, Bradstock RA, Puotinen ML (2011) Assessing the sensitivity
- of MODIS to monitor drought in high biomass ecosystems. Remote Sens Environ
- 545 115:2626–2639.
- 546 Ceccato P, Flasse S, Tarantola S, Jacquemoud S, Grégoire JM (2001) Detecting
- 547 vegetation leaf water content using reflectance in the optical domain. Remote Sens
- 548 Environ 77:22–33.
- 549 Cheney P, Sullivan A (1997) Grassfires fuel, weather and fire behaviour. CSIRO
- 550 Publishing, Collingwood
- 551 Clifford MJ, Royer PD, Cobb NS, Breshears DD, Ford PL (2013) Precipitation
- 552 Thresholds and Drought-Induced Tree Die-off: Insights from Patterns of Pinus Edulis
- 553 Mortality along an Environmental Stress Gradient. New Phytol 200: 413–421.
- 554 Cochard H, Lemoine D, Dreyer E (1999) The effects of acclimation to sunlight on the
- 555 xylem vulnerability to embolism in *Fagus sylvatica* L. Plant Cell Environ 22: 101–108.

- 556 Czúcz B, Gálhidy L, Mátyás C (2011) Present and forecasted xeric climatic limits of
- beech and sessile oak distribution at low altitudes in Central Europe. Ann For Sci 68:99–
- **558** 108.
- 559 Engelbrecht BMJ, Kursar TA, Tyree MT (2005) Drought effects on seedling survival in a
- tropical moist forest. Trees Struct Funct 19: 312–321.
- 561 Epron D, Dreyer E (1993) Long-term effects of drought on photosynthesis of adult oak
- trees [Quercus petraea (Matt.) Liebl. and Quercus robur L.] in a natural stand. New
- 563 Phytol 125:381–389.
- Franch B, Vermote EF, Sobrino JA, Fédèle E (2013) Analysis of Directional Effects on
- 565 Atmospheric Correction. Remote Sens Environ 128: 276–288.
- 566 Geßler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007)
- 567 Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees
- 568 21:1–11.
- 569 Glenn EP, Huete AR, Nagler PL, Nelson SG (2008) Relationship between remotely-
- 570 sensed vegetation indices, canopy attributes, and plant physiological processes: What
- vegetation indices can and cannot tell us about the landscape. Sensors 8:2136–2160.
- 572 Hlásny T, Barcza Z, Fabrika M, Balázs B, Churkina G, Pajtík J, Sedmák R, Turčáni M
- 573 (2011a) Climate change impacts on growth and carbon balance of forests in Central
- 574 Europe. Clim Res 47:219–236.
- 575 Hlásny T, Křístek Š, Holuša J, Trombik J, Urbaňcová N (2011b) Snow disturbances in
- secondary Norway spruce forests in Central Europe: Regression modeling and its
- 577 implications for forest management. For Ecol Manage 262:2151–2161.
- 578 Hmimina G, Dufrêne E, Pontailler J.-Y, Delpierre N, Aubinet M, Caquet B, de Grancourt
- 579 A, Burban B, Flechard C, Granier A, Gross P, Heinesch B, Longdoz B, Moureaux C,
- 580 Ourcival J-M, Rambal S, Saint André L, Soudani K (2013) Evaluation of the Potential of

- 581 MODIS Satellite Data to Predict Vegetation Phenology in Different Biomes: An
- 582 Investigation Using Ground-Based NDVI Measurements. Remote Sens Environ 132:
- 583 145–158.
- Ji L, Peters AJ (2003) Assessing vegetation response to drought in the northern Great
- 585 Plains using vegetation and drought indices. Remote Sens Environ 87:85–98.
- 586 Kotarba AZ (2009) A comparison of MODIS-derived cloud amount with visual surface
- 587 observations. Atmos Res 92: 522-530.
- 588 Lakatos F, Molnár M (2009) Mass mortality of beech in South-West Hungary. Acta
- 589 Silvatica & Lignaria Hungarica, 5:75 82.
- 590 Le Dantec V, Dufrêne E, Saugier B (2000) Interannual and spatial variation in maximum
- leaf area index of temperate deciduous stands. For Ecol Manage 134:71–81.
- 592 Leuschner C, Backes K, Hertel D, Schipka F, Schmitt U, Terborg O, Runge M (2001)
- 593 Drought responses at leaf, stem and fine root levels of competitive Fagus sylvatica L. and
- 594 *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For Ecol Manage 149:33–46.
- 595 Leuzinger, S, Zotz G, Asshoff R, Körner C (2005) Responses of deciduous forest trees to
- severe drought in Central Europe. Tree Physiol 25:641–650.
- 597 Lobo A, Maisongrande P, Coret L (2010) The impact of the heat wave of summer 2003 in
- 598 SW Europe as observed from satellite imagery. Phys Chem Earth, Parts A/B/C 35:19–24.
- 599 Mátyás C, Berki I, Czúcz B, Gálos B, Móricz N, Rasztovits E (2010) Future of Beech in
- 600 Southeast Europe from the Perspective of Evolutionary Ecology. Acta Silv Lign Hung
- 601 6:91–110.
- 602 McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J,
- 603 West A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality
- during drought: Why do some plants survive while others succumb to drought? New
- 605 Phytol 178:719–739.

- 606 Myneni RB, Williams DL (1994) On the relationship between FPAR and NDVI. Remote
- 607 Sens Environ 49:200–211.
- 608 Nahm M, Matzarakis A, Rennenberg H, Geßler A (2007) Seasonal courses of key
- parameters of nitrogen, carbon and water balance in European beech (*Fagus sylvatica* L.)
- 610 grown on four different study sites along a European North–South climate gradient
- 611 during the 2003 drought. Trees 21:79–92.
- 612 Polle A, Schwanz P, Rudolf C (2001) Developmental and seasonal changes of stress
- responsiveness in beech leaves (*Fagus sylvatica* L.). Plant Cell Environ 24:821–829.
- 614 Plaut J, Wadsworth WD, Pangle R, Yepez EA, McDowell NG, Pockman WT (2013)
- 615 Reduced Transpiration Response to Precipitation Pulses Precedes Mortality in a Piñon-
- 516 Juniper Woodland Subject to Prolonged Drought. New Phytol 200: 375–387.
- 617 Raftoyannis Y, Radoglou K (2002) Physiological responses of beech and sessile oak in a
- 618 natural mixed stand during a dry summer. Ann Bot 89:723–730.
- 619 Renaud JP, Nageleisen LM (2005) Results from the European Network For Damage
- 620 Monitoring. Bilan de la santé des forêts en 2004, 2005, Département de la santé des
- 621 forêts, Paris.
- 622 Rennenberg H, Loreto F, Polle A, Brilli F, Fares S, Beniwal RS, Gessler A (2006)
- 623 Physiological Responses of Forest Trees to Heat and Drought. Plant Biology 8:556–571.
- 624 Rouault, G., J.N. Candau, F. Lieutier, L.M. Nageleisen, J.C. Martin, and N. Varzée. 2006.
- Effects of drought and heat on forest insect populations in relation to the 2003 drought in
- 626 Western Europe. Ann For Sci 63:613–624.
- 627 Sack L 2004. Responses of temperate woody seedlings to shade and drought: Do trade-
- 628 offs limit potential niche differentiation? Oikos 107: 110–127.

- 629 Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011)
- 630 Drought matters Declining precipitation influences growth of Fagus sylvatica L. and
- 631 *Quercus robur* L. in north-eastern Germany. For Ecol Manage 262:947–961.
- 632 Shuai et al. 2013
- 633 Soudani K, Hmimina G, Delpierre N, Pontailler J-Y, Aubinet M, Bonal D, Caquet B, de
- 634 Grandcourt A, Burban B, Flechard C, Guyon D, Granier A, Gross P, Heinesh B, Longdoz
- B, Loustau D, Moureaux C, Ourcival J-M, Rambal S, Saint André L, Dufrêne E (2012)
- 636 Ground-based Network of NDVI measurements for tracking temporal dynamics of
- 637 canopy structure and vegetation phenology in different biomes. Remote Sens Environ
- 638 123:234–245.
- 639 Thomsen JE, Bohrer G, Matheny AM, Ivanov VY, He L, Renninger HJ, Schäfer KVR
- 640 (2013) Contrasting Hydraulic Strategies during Dry Soil Conditions in *Quercus rubra*
- and *Acer rubrum* in a Sandy Site in Michigan. Forests 4, 1106-1120.
- 642 Vacchiano, G., M. Garbarino, E.B. Mondino, and R. Motta. 2012. Evidences of drought
- stress as a predisposing factor to Scots pinedecline in Valle d'Aosta (Italy). Eur J For Res
- **644** 131:989–1000.
- 645 Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic
- 646 plasticity. New Phytol 176:749–63.
- van der Salm C, Reinds GJ, de Vries W (2007) Water balances in intensively monitored
- 648 forest ecosystems in Europe. Environ Pollut 148:201–212.
- 649 Vicente-Serrano SM, Beguería S, Lorenzo-Lacruz J, Camarero JJ, López-Moreno JI,
- 650 Azorin-Molina C, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A (2012) Performance
- of Drought Indices for Ecological, Agricultural, and Hydrological Applications. Earth
- 652 Interact 16:1–27.

- 653 Wamelink GWW, Wieggers HJJ, Reinds GJ, Kros J, Mol-Dijkstra JP, van Oijen M, de
- Vries W (2009) Modelling impacts of changes in carbon dioxide concentration, climate
- and nitrogen deposition on carbon sequestration by European forests and forest soils. For
- 656 Ecol Manage 258:1794–1805.
- 657 Wang J, Rich PM, Price KP (2003) Temporal responses of NDVI to precipitation and
- temperature in the central Great Plains, USA. Int J Remote Sens 24:2345–2364.
- 659 Wang LL, Qu JJ, Xiong XX, Hao XJ (2009) Analysis of seven-year moderate resolution
- 660 imaging spectroradiometer vegetation water indices for drought and fire activity
- assessment over Georgia of the United States. J Appl Remote Sens 3:033555.
- 662 Weber P, Bugmann H, Pluess AR, Walthert L, Rigling A (2012) Drought response and
- 663 changing mean sensitivity of European beech close to the dry distribution limit. Trees
- 664 27:171–181.

Table 1 Criteria for the selection of forest stands used for the assessment of heat and drought effect on beech and oak stands

Criterion	Limits
Percentage of investigated species	>99%
Altitude	<670 m a.s.l. for oak; <850 m a.s.l. for beech
Relief aspect	southern slopes
Stand age	>50 years
Stand age Distance from meteorological station	<15 km from station with air temperature data;
Distance from meteorological station	< 7 km from station with precipitation data
Vertical structure of stands	Single-storey stands only
Soil and bedrock	Homogenous across the pixels within group

676 Table 2 Descriptive data of beech and oak forest stands covered by the clusters of

677 MODIS pixels used in the investigation NDVI response to drought and heat stress. Mean

678 values and standard deviations are given.

-	EP	NoP	Altitude	Slope	Aspect	Age	Density	DifAltT	DifAltP	DifT	DifP
	24	1101		-	-	50			2		Dim
			[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
PLOTS	5	4	655±72	29±2.6	150±36	121±9	0.6±0.1	254	315	9,177	3,331
NTAL	6	4	688±63	31±3.2	192±38	139±3	0.7±0.0	254	650	11,047	2,585
ERIME	7	7	714±68	29±1.8	174±62	103±6	0.8±0.0	411	502	7,902	3,283
BEECH EXPERIMENTAL PLOTS	8	5	742±106	26±4.3	138±19	114±7	0.7±0.0	875	583	5,535	4,620
BEE	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
-STOL	3	4	544±8	6±3.6	201±36	54±2	0.9±0.1	139	241	13,290	5,987
OAK EXPERIMENTAL PLOTS+	4	10	574±57	15±2.4	176±41	83±17	0.7±0.0	318	338	2,676	2,241
RIMEN	5	7	186±7	2±0.4	141±16	71±13	0.7±0.0	110	117	8,550	6,878
K EXPE	6	6	376±24	8±1.8	176±63	85±1	0.8±0.0	100	160	9,005	2,923
OA]	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

⁶⁷⁹

Abbreviations: EP - Experimental Plot; NoP - Number of MODIS Pixels covering an EP; Slope - mean relief slope within an EP; Aspect - mean relief 680 aspect within an EP; Density - mean stand density within an EP; DiffAltT - mean altitudinal difference between an EP and meteorological stations used 681 for the air temperature interpolation; DifAltP - altitudinal difference between an EP and the meteorological station used for the calculation of rainless

682 periods; DiftT - mean horizontal distance between an EP and meteorological stations used for the calculation of air temperature-related extremes; DifP

683 - mean horizontal distance between an EP and the meteorological station used for the calculation of rainless periods

685 Table 3 Descriptive statistics of maximum observed NDVI declines, described in terms 686 of percentage decline from the total NDVI amplitude, that occurred as a result of potential 687 drought and heat stress during the period 2000–2010 in oak and beech stands in Central 688 Europe. The variable describes the maximum stress induced by climatic factors to beech 689 and oak that was recorded using MODIS imagery.

									690
		Ν	Mean	Med	Min	Max	0.25	0.75	690 StDev
Ι	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

- 694 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

696 Central Europe

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	I	BEECH E	EXPERIN	1ENTAL	PLOTS			OAK E	XPERIM	IENTAL	PLOTS	
Variables	Ν	Mean	Med	Min	Max	StDev	Ν	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

698 Abbreviations: GDD –growing degree days; Drt – length of drought period; Age – mean stand age; Elev – mean stand elevation; Tavg – mean air

699 temperature during a drought period; Tmax – maximum air temperature during a drought period; Tmin – minimum air temperature during a drought

700 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

701 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

702 20°C (or above 23°C, 26°C, 29°C, 32°C, 35°C), which occurred during a stress episode

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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

	Training	Testing	Validation
Beech	$0.86\pm6\%$	$0.82\pm8\%$	$0.93\pm0.6\%$
Oak	$0.88 \pm 1.0\%$	$0.81\pm9\%$	$0.96\pm0.3\%$

715 **Table 6** Mean sensitivity scores of explanatory variables produced by 15 best-performing Neural Networks. The scores indicate the predictive power of

resplanatory variables in explaining the observed declines in NDVI values induced by heat and drought stress. The higher the score, the closer the relationship

717 between the explanatory and the dependent variables.

718

BEECH	EXPERIM	ENTAL PL	OTS														
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	ГS														
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-Tma
>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

719 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; Tmin – minimum air

720 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)

721 – 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

722

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			
730	Fig. 2 Seasonal course of MODIS-NDVI observations from a single stand in one year (dots). Arrow		
731	identifies a typical episode of NDVI decline symptomatic of climatic stress. $NDVI_{max}$ represents the		
732	mean of 2-4 NDVI observation immediately preceding a stress episode (local maximum), $NDVI_{stress}$ is		
733	the value at the end of a stress episode, and $NDVI_{min}$ is the lowest NDVI value observed in local		
734	conditions.		
735			
736	Fig. 3 Univariate relationships between maximum NDVI declines and predictor variables which were		
737	identified as the most influential by neural networks-based regression modelling in oak stands.		
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		

745	Appendix	captions
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746 Appendix A

Example of experimental plots used for the investigation of MODIS-NDVI responses to climatic
stress. Each experimental plot in our experimental design consists of 4-13 MODIS pixels (250×250m)

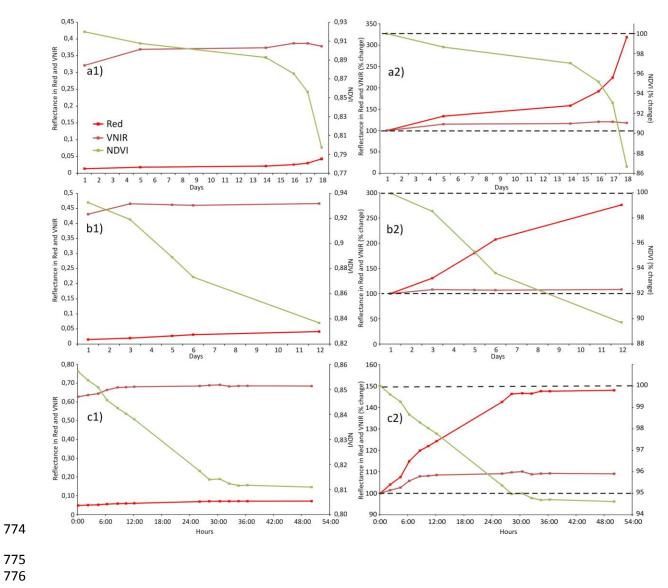
750 Appendix B

- 751 An example of declining sequences of MODIS-NDVI identified in NDVI time series for selected
- beech and oak dominated MODIS pixels for the period 2000-2010. Such sequences are indicative of
- renvironmental stress affecting the physiological performance and spectral reflectance of vegetation.

755 Appendix C

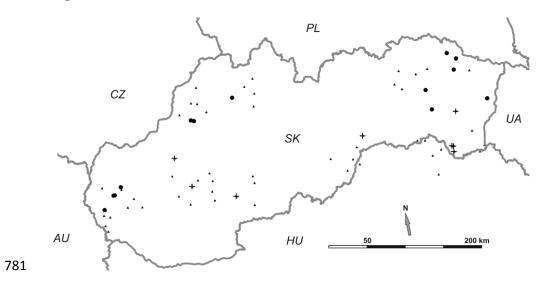
Reflectance of mature homogenous stands within two MODIS pixels with spatial resolution 250×250

- 757 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.
- 762 Spectral reflectance values in panes C) were measured by the LI-1800 Portable
- 763 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.
- 768 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
- 773 distinguished from intra-seasonal vegetation dynamics.

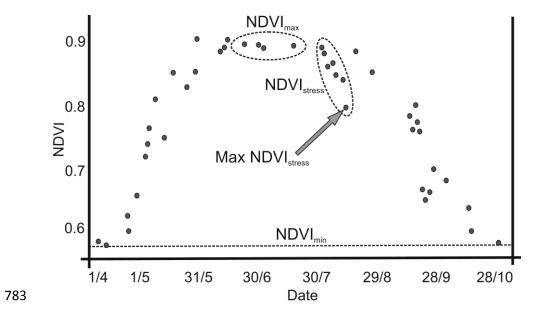




780 Figures









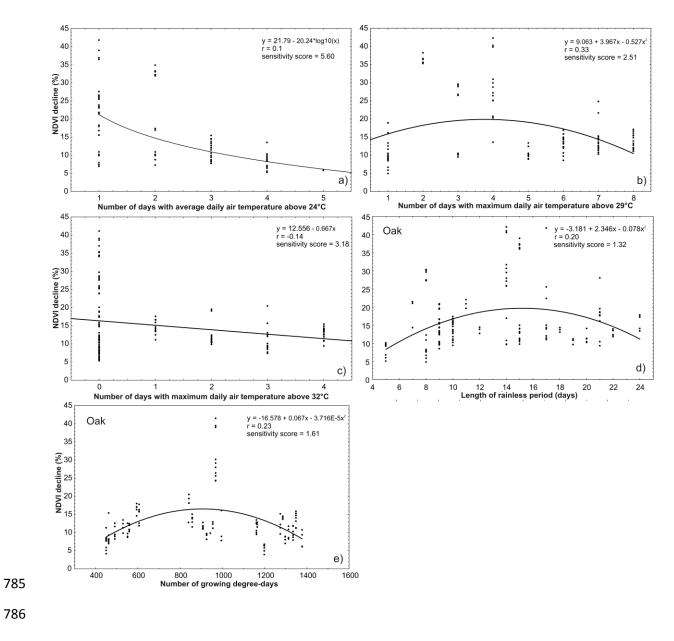


Fig. 3

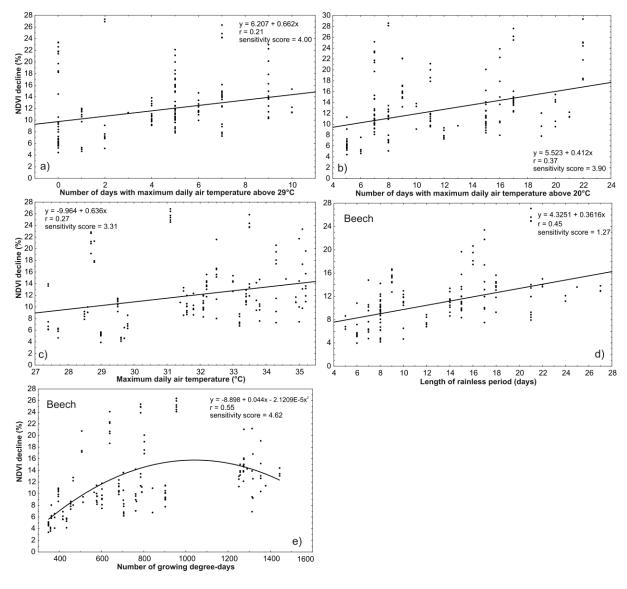


Fig. 4

