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Impact of land-use intensity on the relationships between vegetation indices, photosynthesis and biomass of intensively and extensively managed grassland fens

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Abstract

Vegetation indices are widely used as model inputs and for non-destructive estimation of biomass and photosynthesis, but there have been few validation studies of the underlying relationships. To test their applicability on temperate fens and the impact of management intensity, we investigated the relationships between normalized difference vegetation index (NDVI), leaf area index (LAI), brown and green above-ground biomass and photosynthesis potential (PP). Only the linear relationship between NDVI and PP was management independent ($R^2 = 0{\cdot}53$). LAI to PP was described by a site-specific and negative logarithmic function ($R^2 = 0{\cdot}07$–$0{\cdot}68$). The hyperbolic relationship of LAI versus NDVI showed a high residual standard error (s.e.) of 1·71–1·84 and differed between extensive and intensive meadows. Biomass and LAI correlated poorly ($R^2 = 0{\cdot}30$), with high species-specific variability. Intensive meadows had a higher ratio of LAI to biomass than extensive grasslands. The fraction of green to total biomass versus NDVI showed considerable noise (s.e. = 0·13). These relationships were relatively weak compared with results from other ecosystems. A likely explanation could be the high amount of standing litter, which was unevenly distributed within the vegetation canopy depending on the season and on the timing of cutting events. Our results show there is high uncertainty in the application of the relationships on temperate fen meadows. For reliable estimations, management intensity needs to be taken into account and several direct measurements throughout the year are required for site-specific correction of the relationships, especially under extensive management. Using NDVI instead of LAI could reduce uncertainty in photosynthesis models.

Keywords: ground validation, remote sensing, normalized difference vegetation index, photosynthesis, leaf area index, biomass, peatlands, optical vegetation indices

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Introduction

Vegetation characteristics and productivity are important inputs for various statistical (empirical) as well as process-oriented models, leading to an increasing demand for non-destructive measurement methods and estimations on a national or global scale. Several methods have been developed and are widely used to estimate vegetation characteristics from optical measurement methods in the field and from satellite data, but these methods have not been validated sufficiently. The relationships between the indices and vegetation characteristics are known to be ecosystem specific (Knyazikhin *et al.*, 1998). Investigations of these relationships on both intensively and extensively managed temperate fen grasslands are, to our knowledge, still lacking. Grassland is the most common land-use type on peatlands in Central Europe. Its carbon balance is extremely important in the context of greenhouse gas mitigation due to its role in carbon sequestration and its potential for high carbon dioxide (CO_2) emissions (Drösler *et al.*, 2008). Non-destructive estimations of vegetation characteristics can help to improve understanding and modelling of the carbon balance of these ecosystems. In this study, we therefore investigated the relationships between common vegetation indices and vegetation characteristics

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including biomass on managed grasslands in a temperate fen.

Vegetation indices and plant characteristics are very important for ecosystem and carbon models. This importance is due to the various functionalities of the plant for many processes; for example, leaf area index (LAI) or amount of biomass affects plant respiration (De Vries, 1975), evapotranspiration (Leuning *et al.*, 2008), microclimate (Peacock, 1975), temperature isolation between soil and atmosphere (Kätterer and Andrén, 2009) and the amount of litter and root exudates, which provide fresh substrate for decomposers (Kuzyakov *et al.*, 2000). The potential of the plant to absorb radiation is a key component for modelling photosynthesis (Monteith, 1972) and this is related to greenness indices like the normalized difference vegetation index (NDVI; Gamon *et al.*, 1995). Plant biomass provides a measure of actual accumulated photosynthetic net production (Monteith, 1972). The importance of LAI has been emphasized in plant productivity models (Cowling and Field, 2003). LAI might also be an important parameter for empirical models: for example, maximum LAI could explain, to a large extent, the between-site variability in annual gross primary production (GPP) and net ecosystem exchange (NEE) of twelve northern peatlands (Lund *et al.*, 2009) and eight forests (Lindroth *et al.*, 2008).

Optical vegetation indices are usually much less expensive and are easier to measure compared with more direct variables like carbon uptake. NDVI is directly calculated from spectral reflectance in different wavebands and is therefore available on a global scale from satellite images. LAI can be estimated by direct and indirect techniques (methods are reviewed in Breda, 2003; Jonckheere *et al.*, 2004). Direct measurements are destructive and workload intensive, but allow the measurement of the green (photosynthetically active) plant parts [referred to subsequently as green area index (GAI)]. An easy-to-measure and commonly used indirect method is the determination of LAI using a ceptometer to measure the light transmission through a canopy, which also includes dead and senescent (brown) above-ground parts of the vegetation [referred to subsequently as plant area index (PAI)]. Plant area divided by the plant weight is referred to as specific plant area (SPA). An indirect method for providing GAI on larger scales is to calculate it from satellite-derived indices like NDVI (Rossini *et al.*, 2012). NDVI has been shown to be related to photosynthesis (Gianelle *et al.*, 2009), biomass (Vescovo *et al.*, 2012) and fraction of green to total biomass (green ratio; Gianelle and Vescovo, 2007). These dependencies are, however, known to be specific to particular biomes (Heinsch *et al.*, 2006), plant species and vegetation types (Anderson, 1995; Wilson *et al.*, 2007), and also to plant architecture and soil (Darvishzadeh *et al.*, 2008) and site conditions (Kross *et al.*, 2013). Therefore, shape parameters of the relationships need to be developed, and the dependencies need to be validated for each ecosystem type.

Many studies have investigated dependencies between satellite-derivable vegetation indices and plant characteristics or photosynthesis for different types of grasslands (Fan *et al.*, 2009; Wohlfahrt *et al.*, 2010) and also on northern peatlands (Kross *et al.*, 2013), but few such studies have included nutrient-rich wetlands (Rendong and Jiyuan, 2002). There are, to our knowledge, no reported investigations of these relationships for managed temperate grassland fen, a class of vegetation communities that are characterized by having greater productivity than boreal peatlands but are usually less intensively managed than many types of grasslands on mineral soils. The carbon balance and, consequently, the relationships between vegetation indices and biophysical vegetation characteristics such as input for carbon models and statistical analysis are of extraordinary importance on managed grassland fens, as they have potential to be hot spots for greenhouse gas emissions, depending on their land use and drainage intensity (Drösler *et al.*, 2008).

Plant communities and different species vary in their spectral reflectance (Anderson, 1995) and temporal patterns in reflectance (Gamon *et al.*, 1995). Management affects plant productivity and plant community composition through harvest, nutrient input and drainage (Wedin, 1996) and is therefore expected to have an impact on reflectance indices like NDVI and its relation to different vegetation characteristics. Extensively managed meadows, in particular, can have large amounts of standing litter which can alter the biophysical interpretation of vegetation indices (van Leeuwen and Huete, 1996). Further, they host species that have differences in leaf greenness. It was expected that this would affect the relationships between different vegetation characteristics and optically derived indices.

The objective of this study was to investigate the impact of management intensity on the relationships between vegetation indices and vegetation characteristics including potential photosynthesis (PP) on temperate grassland fens. Specifically, we wanted to test the potential to use:

- NDVI as a proxy for PP, LAI, biomass and green ratio; and
- PAI and GAI as a proxy for biomass and PP.

Accordingly, we investigated biomass, LAI, PP and ground-measured and satellite-derived NDVI at five selected meadows with different management regimes in a fen in southern Germany.

Methods

Site description

The Freisinger Moos (48°22′N, 11°40′E; elevation 449 m a.s.l.) is a groundwater-fed fen in southern Germany, located between the River Isar in the south and a hilly area on its northern boundary (Schober and Stein, 2008). Maximum peat depths reach 7 m (Schober and Stein, 2008). The peatland extends over an area of 1030 ha. The main land-use type is grassland (66%), with 60% intensively managed with up to four cuts per year, while 4% consists of protected biotopes (Schober and Stein, 2008).

Five sites were selected on several land parcels of different management intensity, ranging from three cuts per year and a fertilization rate of up to 252 kg N ha^{-1} $year^{-1}$, to extensively managed grasslands, including protected biotopes that have only one management cut every second year in late autumn and no fertilization (Table 1). Two of the sites that clearly differed in their vegetation composition were located on the same parcel (E3).

Each site consisted of gas-measurement plots and a small area outside the plots (vegetation patch) where all other variables were sampled. The vegetation patches were necessary because the chamber plots were surrounded by boardwalks and storage for chambers and other instruments, and the presence of these could have biased the satellite NDVI. Further, the vegetation around the chamber plots was kept short for easy handling of the chamber, and the 3-cm-high soil

Table 1 Characteristics of sites with available gas flux measurements.

Parcel	Management	Mean water table (cm)	Dominant vegetation in June 2012 at the chamber plots	Comment
E1	Natural monument, water level restored, 1 cut every second year during late autumn	−11	*Carex panicea* (43%), *Allium suaveolens* (9%), *Potentilla erecta* (4%), *Schoenus ferrugineus* (4%), *Phragmites australis* (4%), *Cirsium palustre* (2%)	Two sites with slightly different elevation, but no clear difference in vegetation. The mean of both sites was used
E2	Protected biotope, drained, 1 cut per year during late autumn	−32	*Filipendula ulmaria* (30%), *Poa pratensis* (20%), *Anthoxanthum odoratum* (17%), *Galium mollugo* (11%), *Carex nigra* (7%), *Luzula campestris* (5%), *Cirsium oleraceum* (3%), *Peucedanum palustre* (3%), *Rumex acetosella* (2%), *Cerastium holosteoides* (2%)	Four sites with water and temperature manipulation, but only the control site was used
E3a	Hay meadow, drained, 1 cut per year during summer	−25	*Anthoxanthum odoratum* (40%), *Carex nigra* (40%), *Plantago lanceolata* (5%), *Ajuga reptans* (3%), *Galium mollugo* (2%), *Rumex acetosella* (2%)	Same parcel as E3b, but clearly different vegetation
E3b	Hay meadow, drained, 1 cut per year during summer	−20	*Carex vesicaria* (87%), *Galium uliginosum* (3%), *Alopecurus pratensis* (2%), *Poa trivialis* (2%), *Phragmites australis* (2%)	Same parcel as E3a, but clearly different vegetation
I1	Intensive meadow, 2–3 cuts per year, drained, fertilized with 50 kg N ha^{-1} $year^{-1}$	−21	*Poa trivialis* (43%), *Ranunculus repens* (20%), *Trifolium pratense* (17%), *Alopecurus pratensis* (8%), *Festuca pratensis* (4%)	GPP data not available in 2011
I2	Intensive meadow, 2–3 cuts per year, drained, fertilized with 110 kg N ha^{-1} $year^{-1}$	−57	*Dactylis glomerata* (29%), *Poa trivialis* (26%), *Lolium perenne* (14%), *Taraxacum officinalis* (8%), *Cerastium holosteoides* (4%), *Galium mollugo* (4%), *Alopecurus pratensis* (4%), *Trifolium pratense* (4%)	Four sites differing in fertilization, but only the control site was used
I3	Intensive meadow, 3 cuts per year, drained, fertilized 181 kg $year^{-1}$	−41	*Alopecurus pratensis* (63%), *Poa trivialis* (29%)	Four sites with water and temperature manipulation, but only the control site was used

collars of the chamber plots can bias the ceptometer measurements. The patches were selected to represent similar vegetation to that in the plots. They were located at a distance of at least 5 m from the chamber-site areas and had a minimum size of 50 m^2. Due to high spatial variability in the vegetation on extensive meadows, some additional patches were selected that did not represent a chamber site, but included other dominant vegetation types on the parcel. Measurements of PAI and NDVI were recorded in the patches and additionally in the chamber plots, but values from the plots were only used for correlations with PP.

Measurements

Photosynthesis

Flux sampling campaigns were performed during 2010 and 2011 (for site I1, only in 2010) according to the methods described by Eickenscheidt *et al.* (2015). NEE and ecosystem respiration were measured with transparent and opaque chambers (closed dynamic manual chamber system) at three replicated plots of 75 cm × 75 cm on each site under clear sky conditions. CO_2 fluxes, photosynthetically active radiation (PAR) and soil temperatures were sampled repeatedly from sunrise to late afternoon to cover the full range of these parameters in the course of the day. CO_2 fluxes were derived from CO_2 concentrations and were measured with infrared gas analysers (LI-820, LI-COR, Lincoln, NE, USA). For each site and each sampling day, a temperature-dependent ecosystem respiration model was calculated according to Lloyd and Taylor (1994). Modelled respiration was then subtracted from measured NEE to obtain GPP. A GPP model based on a Michaelis–Menten-type rectangular hyperbolic function as proposed by Falge *et al.* (2001) was fitted for each measurement day. From the GPP model, the photosynthesis at a theoretical photosynthetic photon flux density (PPFD) of 2000 μmol m^{-2} s^{-1} was derived. This corresponds to the photosynthesis potential (PP) of the plant in its current developmental stage at the specified light level and was used in all comparisons with vegetation indices. We followed the atmospheric sign convention in which a negative sign indicates CO_2 uptake.

Satellite NDVI

From April 2010 until November 2011, a total of twenty-three RapidEye images of Level 3A were provided by the RapidEye Science Archive Project (RESA, 2016) with a spatial resolution of 5 m, with sixteen images from 2011. Geometric and atmospheric correction was performed using ATCOR 3 implemented in PCI Geomatica 10.3, as described by Elatawneh *et al.* (2013). Only cloud-free pixels were taken into account. Values within 3 d after harvest were not included to avoid effects from hay drying on the fields. The normalized difference vegetation index was calculated in ArcGis (ESRI) version 10.2.0.3348 by the equation:

$$\mathrm{NDVI} = \frac{R_{\mathrm{NIR}} - R_{\mathrm{RED}}}{R_{\mathrm{NIR}} + R_{\mathrm{RED}}} \tag{1}$$

where R_{NIR} and R_{RED} indicate the reflectance in the near-infrared (760–850 nm, channel 5) and the red (630–685 nm, channel 3) wavebands respectively. For comparisons with PP, NDVI values were gap-filled by linear interpolation between two consecutive measurements if no harvest or year shift occurred.

Ground NDVI and PAI

Sampling campaigns for NDVI and PAI were performed every 2–4 weeks between April 2011 and July 2012. Samples were taken less frequently at those vegetation patches that did not represent a gas flux measurement site. At each sampling day, NDVI and PAI were measured at five randomly selected locations per vegetation patch and on each of the three chamber plots per flux measurement site. Measures of NDVI and PAI and biomass samples were taken from the same spots in the vegetation patches. Three replicated measurements were taken for LAI and NDVI at each spot, and resulting values were averaged. Measurements were performed within 3·5 h (2·5 in winter) on either side of solar noon under clear sky conditions. PP and satellite-derived NDVI were often sampled on different dates. Therefore, NDVI and LAI values were linearly interpolated between each pair of measurement points to match the dates of PP sampling. In cases of harvest or year shift between two measurement points, the data were excluded.

Ground-based NDVI was sampled using a handheld spectroradiometer with two four-channel sensors (SKR 1850; Skye Instruments Ltd, Powys, UK) simultaneously measuring incident and reflected light in the same wavebands as RapidEye for the red and the near-infrared channel. The sensor was held 160 cm above the soil to capture a surface with a diameter of 70 cm to fit the dimensions of the chamber plots. In these plots, the pole on which the sensors were mounted was placed on a marked position, to ensure that the white soil frames for the chambers were not inside the captured surface. NDVI was calculated according to the Equation 1.

A ceptometer-based canopy analysis system (SunScan system SS1, Delta-T Devices Ltd, Cambridge, UK) was used for PAI measurements. The SunScan system measures both diffuse and direct radiations. It includes a beam fraction sensor placed above the vegetation for sampling incident PAR. Simultaneously, PAR under the canopy is collected by a 1-m-long probe including sixty-four photodiodes. The average of all sixty-four diodes was used for PAI calculation. A leaf absorption value of 0·85, a random spherical distribution of leaves and a correction term of 0·3 to account for the height of the probe were assumed for PAI calculations, as suggested in the user manual (Webb *et al.*, 2008). A detailed description of how the system calculates PAI is given by Webb *et al.* (2008).

At the chamber plots, three replicated measurements at each diagonal at each site plot were averaged. To account for the bias due to the soil frames and shorter vegetation around the plots, the values were corrected by the slope of a linear regression between PAI from chamber plots and PAI from the corresponding patch, whereas the regression line was forced through zero. Only PAI values from spots in a patch were used for the correction that did not differ in NDVI by more than 0·05 compared with the average NDVI measured at the corresponding site. The corrected PAI values were only used for comparison with PP. For all other correlations, PAI and NDVI values from the vegetation patches were employed.

Biomass, green ratio, GAI

A total of 186 biomass samples were collected between April 2011 and July 2012 on the same dates and locations as the PAI and NDVI measurements. Three samples were taken at each vegetation patch on each measurement date. Green mosses and all aboveground plant parts attached to a plant were cut with a knife within a frame spanning 20 cm on both sides of the SunScan probe, leading to a sample size of 100 cm × 40 cm. In cases of very homogenous vegetation and PAI values lower than 1·5 $m^2\ m^{-2}$, a smaller sample size of 40 cm × 40 cm was used. The samples were stored in plastic bags and frozen until further processing. Each sample was mixed to achieve a homogeneous distribution of brown and green leaves. Then, around 0·25 of each sample was sorted into green and brown plant parts, weighed separately and later multiplied by the total weight to estimate the dry weight of brown and green biomasses. The samples were oven-dried at 60°C for at least 48 h before weighing. GAI was calculated from PAI by multiplying it by the percentage of green leaves. To determine GAI at the chamber plots, where destructive sampling was not possible, PAI was multiplied by the green ratio, which was derived from the relationship between green ratio and NDVI over all samples.

Analyses and statistics

All statistical analyses were carried out using R software, version 3.03 (R Core Team, 2014). The relationships between each variable pair were analysed with respect to regression coefficients, residual standard errors (s.e.) and a partial *t*-test providing the coefficients of determination (R^2) by simple linear regression (lm function in the stats package; R Core Team, 2014). Therefore, nonlinear relationships were linearized by simple exponential or logarithmic transformations. The coefficients for these transformations were derived by fitting a nonlinear least-squares model (fitModel function in the mosaic package; Pruim *et al.*, 2014). Each relationship was tested without transformation, and with logarithmic and simple power transformations: those equations were applied that resulted in the highest R^2 value. If R^2 values were similar, no transformation was applied. The assumption for a *t*-test of normality of model residuals was tested using the Kolmogorov–Smirnov test (ks.test function in the stats package; Lilliefors, 1967; R Core Team, 2014). If the data did not satisfy the necessary requirements, the nonparametric pairwise Wilcoxon rank-sum test (wilcox.test function in stats package; Bauer, 1972; R Core Team, 2014) was used instead of the partial *t*-test. For all statistical tests, a significance level of 0·05 was chosen. Box plots were used to compare the values from intensive and extensive meadows. For time series, the data were classified into groups of 1 month. For the relationships between PAI and NDVI, as well as GAI and NDVI, the NDVI data were classified into intervals of width 0·1. The absence of overlapping notches of two boxes was used as an indication of a significant difference in mean values (McGill *et al.*, 1978).

Results

The usability of vegetation indices as a proxy for biophysical vegetation characteristics varied greatly for the different relationships: Pearson's correlation coefficients ranged from 0·06 for NDVI as a proxy for biomass, up to 0·60 for NDVI as a proxy for green ratio (Table 2). All the relationships were stronger when intensive and extensive meadows were considered separately, except the relationship between NDVI and PP.

Seasonal patterns of NDVI and PAI

Normalized difference vegetation index values at intensive meadows saturated earlier than those at

Table 2 Correlation matrix for all relationships investigated, showing R^2 values for all meadows and for intensive and extensive meadows.

	PAI			NDVI		
	All	Intensive	Extensive	All	Intensive	Extensive
NDVI	0·24	0·33	0·27	–	–	–
PP	0·36	0·48	0·30	0·53	0·34	0·56
Biomass	0·30	0·25	0·42	0·06	0·08	0·13
Green ratio	–	–	–	0·60	0·59	0·63

PAI, plant area index; NDVI, normalized difference vegetation index.

extensive meadows, but both reached similar maxima, close to 1 (Figure 1a). Faster spring growth at intensive meadows was also reflected in PAI values (Figure 1b). The first cuttings on intensive meadows took place before PAI saturation. During winter, intensively managed parcels exhibited a high NDVI (around 0·75), while it was considerably lower on extensive meadows (around 0·6). PAI values decreased towards the end of the year and were lower at intensive meadows compared with extensive meadows during winter.

NDVI as proxy for green ratio

The relationship between NDVI and green ratio was similar between management intensities, but the distribution within the relationship was not (Figure 2): only two samples from intensive meadows had NDVI values lower than 0·7, while more than half had values higher than 0·9. The lowest value for green ratio at intensive meadows was 0·16, with an NDVI value of 0·77, while 53% of the observations showed a green ratio higher than 0·7. In contrast, 28% of the

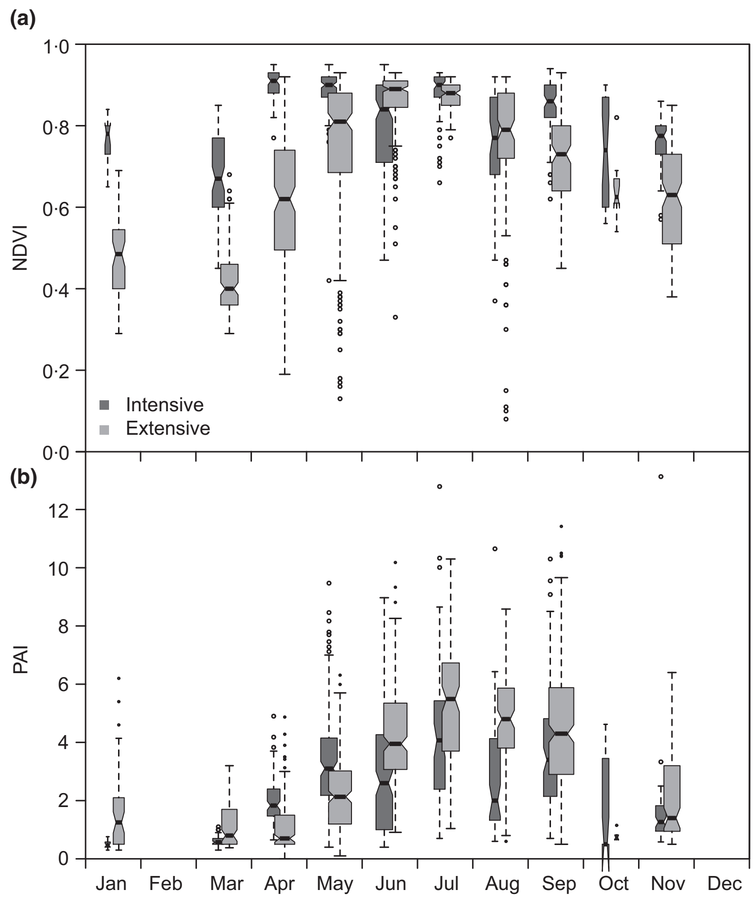

Figure 1 Boxplots of ground normalized difference vegetation index (NDVI) (a) and plant area index (PAI) (b) in the course of the year. The data are grouped in one class for each month of the year, independently of whether sampled in 2011 or 2012. The width of the boxes indicates the number of observations in each category. The maximum width corresponds to 2670 data points, the minimum to 128. Boxplots for intensive meadows are shifted to the left for better visibility.

samples from extensive meadows had NDVI values lower than 0·7, and 21% a green ratio higher than 0·7. Large scatter occurred for low values, especially at extensive meadows where samples with 20–40% brown biomass span a NDVI range from 0·44 to 0·92.

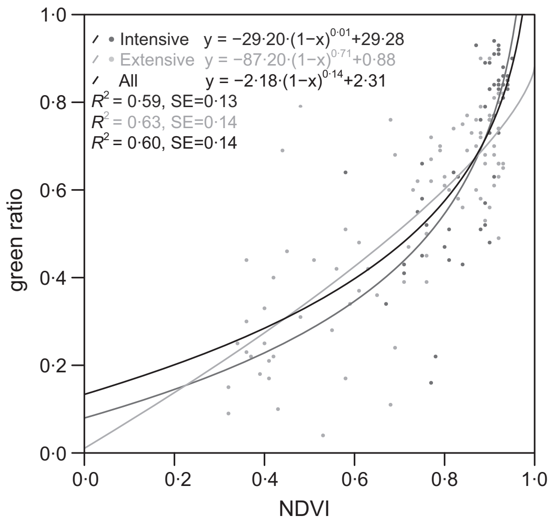

Figure 2 Green ratio for intensively, extensively, and intensively and extensively managed meadows together, measured on several dates throughout the year, plotted against ground normalized difference vegetation index (NDVI), determined at the same spots. The dark grey and the light grey curve correspond to the data points of the intensive and extensive meadows, respectively, whereas the black curve is fitted to the whole data set.

NDVI as proxy for LAI

At both intensive and extensive meadows, NDVI was saturated with high PAI values (Figure 3a). The relationships showed considerable noise, especially at extensive meadows for low and high NDVI values. Intensive meadows showed a similarly large scatter only for NDVI values higher than 0·7.

Extensive meadows had considerably higher mean PAI values compared with intensive meadows for NDVI values lower than 0·9 (Figure 3b). This was also true when GAI values were compared with NDVI values (Figure 3c); however, GAI values on intensive meadows were higher in the NDVI interval between 0·9 and 1.

PAI and NDVI as proxies for biomass

Plants from intensive meadows tended to have a higher SPA compared with those from extensive ones, but the scatter was enormous (Figure 4), and therefore PAI was a poor predictor. NDVI was an even worse predictor for biomass than PAI: a linear correlation for all observations resulted in an R^2 value of 0·06.

NDVI and PAI as proxies for PP

The relationship between PP and NDVI was linear for both satellite- and ground-measured NDVI values, with only small differences between management intensities (Figure 5a). The relationship between PP versus GAI showed strong saturation effects for GAI values higher than 1 (Figure 5b). Differences were

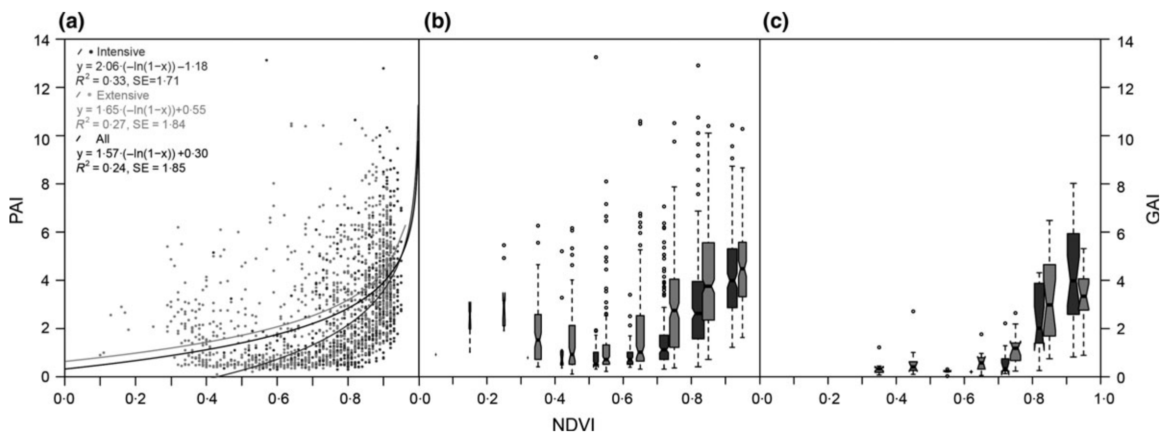

Figure 3 Leaf area index (LAI) plotted against ground normalized difference vegetation index (NDVI) determined for the intensively and extensively managed meadows on several days throughout the year. LAI corresponds to plant area index (PAI) in (a) and (b) but to GAI in (c). The width of the boxes indicates the number of observations in each category. The maximum width corresponds to 374 (b) and 27 (c) data points. Boxplots for intensive meadows are shifted to the left for better visibility.

observed not only between intensive and extensive meadows, but also between different parcels. Intensive meadows had higher PP values at the same GAI values than extensive meadows. Among the extensive meadows, the protected biotope E2 had higher values than the hay meadow E3, while the natural monument E1 had the lowest values.

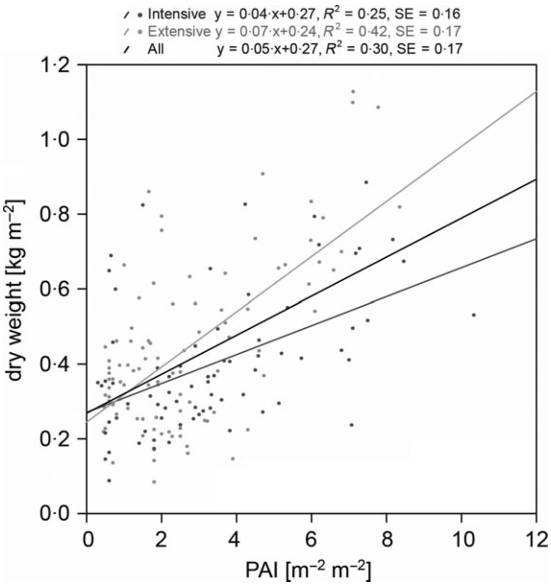

Figure 4 Total biomass plotted against plant area index (PAI) from intensively (dark grey), extensively (light grey), and intensively and extensively managed meadows together (black), measured on several dates throughout the year.

Discussion

Managed grassland fens are the land cover type with the second-highest net climate effect in Europe, just after arable fens; their CO_2 emissions are especially high in Germany, where they are often intensively managed (Drösler *et al.*, 2008). Due to the relevance of vegetation parameters for carbon-related processes, the results of this study have strong implications for CO_2 models that use vegetation indices as input, but also for biomass estimations from remote sensing data and non-destructive methods. The productivity of fens is of interest for management decision-making, as they are of high conservation value due to their significance for biodiversity and endangered species preservation, as well as for flood mitigation and water quality improvement (Mitsch and Gosselink, 2000), especially if management intensity is low. In general, the observed relationships between NDVI or LAI with vegetation characteristics on the temperate fen meadows in the Freisinger Moos were poorer and showed higher scatter compared with relationships that have been reported for other ecosystems. In particular, the widely used LAI was shown to be a poor predictor for biomass and PP and could only poorly be estimated from NDVI. Further, the shapes of the underlying relationships depended on management intensity. Therefore, the application of LAI as model input or biomass proxy on these meadows will result in high uncertainty. NDVI was found to be a better predictor for PP and should thus replace LAI in photosynthesis models. This study further revealed the need for ecosystem-specific validation studies for commonly used relationships between vegetation indices and vegetation

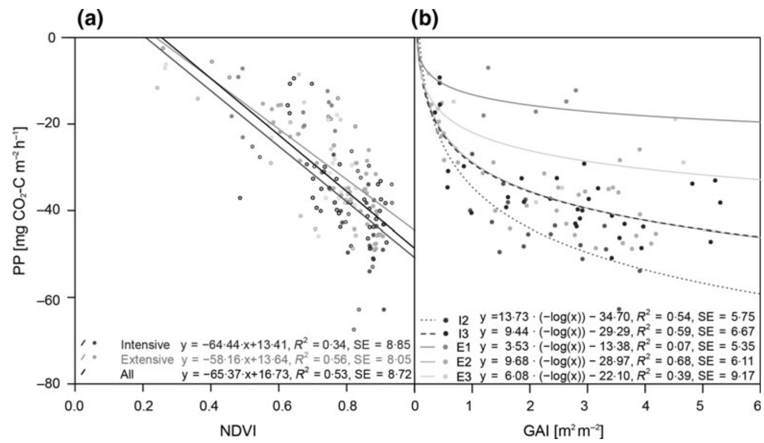

Figure 5 Potential photosynthesis (PP) derived from chamber flux measurements, plotted against normalized difference vegetation index (NDVI) (a) and GAI (b). Open circles represent NDVI from satellite data, whereas closed circles refer to ground NDVI. As the relationships between PP and GAI (b) showed distinct site-specific patterns, they were plotted for each meadow. I2 and I3 are intensively managed; E1, E2 and E3 are extensively managed meadows (cf. Table 1).

characteristics. The results for each relationship are discussed in more detail in the following sections. Uncertainty in the data, resulting from the optical measurement methods, is treated in the last part of the discussion.

Seasonal patterns of NDVI and PAI

Extensive and intensive meadows differed largely in their seasonal patterns of both NDVI and LAI. A higher proportion and different distribution of standing brown biomass might be the main reason for the higher winter PAI and lower winter, spring and autumn NDVI values on extensive meadows compared with intensive meadows, where standing litter was removed by the more frequent cuttings. Also, species-specific reflection might be important. The extensive meadows investigated in this study hosted a larger number of species including some sedge species and reed (*Phragmites australis*; Table 3), which differed visibly from the grass species on intensive meadows by a more grey-blue leaf colour, especially in the spring. Grey-green and yellow-green leaf colours can lead to lower NDVI values compared with green vegetation (Satterwhite and Ponder Henley, 1987), and different reflectance properties were reported for different wetland species (Anderson, 1995). High correlations between NDVI, visible colour, chlorophyll content and leaf nitrogen content have been reported for several grass species (Bell *et al.*, 2004). The close connections between chlorophyll content and red spectrum (Tucker, 1979) used in NDVI calculations, and between leaf chlorophyll and nitrogen content (Gáborčík, 2003) are well-established concepts and might serve as explanations for differences between the fertilized intensive and non-fertilized extensive meadows.

Mapping studies have shown that peatlands can be distinguished from similar ecosystems on mineral soils

Table 3 Standard deviations from site and vegetation patch mean values.

	Average	Max
Ground LAI at vegetation patches and sites	0·51	2·98
Ground NDVI at vegetation patches and sites	0·03	0·18
Satellite NDVI at vegetation patches	0·02	0·12
PP at sites	1·47	8·09
Biomass at vegetation patches	83·30	239·03
Green:brown ratio at vegetation patches	0·08	0·34

LAI, leaf area index; NDVI, normalized difference vegetation index.

by a significantly lower maximum NDVI that is reached at a later date (Gardi *et al.*, 2009). In the present study, the extensive meadows were wetter and consisted of a more peatland-typical vegetation than intensive meadows. Therefore, at extensive meadows we expected lower maximum NDVI values, which would be reached at a later date. However, our results confirmed these differences only with respect to the timing, but not with respect to the magnitude of maximum NDVI values.

NDVI as proxy for green ratio

A potentially useful aspect of the relationship between NDVI and green ratio would be the correction of ceptometer-derived PAI to derive GAI for situations where destructive sampling is either not possible or too time-consuming. NDVI was reported to be a reliable predictor of green ratio, showing a linear relationship without any saturation for several grasslands in the Italian Alps and in New Zealand (Gianelle and Vescovo, 2007). In contrast, the data from the Freisinger Moos showed large scatter, a curved relationship and a rather different distribution within the relationship depending on management intensity. This might be explained by a very heterogeneous litter distribution; during the seasonal growth of graminoids in particular, leaves develop on the surface of the canopy, while lower leaves are shaded and die (Robson, 1973). Hence, brown biomass is located under green leaves and cannot be detected by reflectance measured from above, resulting in a lower green ratio at high NDVI values. This was especially pronounced at the relatively productive site I3, before the first cut took place, and might explain that the curvature of the relationship was bent towards higher NDVI values. In contrast, sedges started yellowing at the leaf tips, leading to brown biomass covering the green parts. Basal plant parts remained green during winter, which was also observed by Saarinen (1998) in a *Carex rostrata* fen. Furthermore, at extensive meadows without a cut in late autumn, a considerable amount of brown standing biomass was still present in spring, when new green leaves emerged under their shade.

NDVI as proxy for LAI

The relationship between NDVI and PAI is especially relevant for the estimation of LAI from remotely sensed data. In our results, the relationship showed larger scatter compared with previous studies (Gamon *et al.*, 1995; Darvishzadeh *et al.*, 2008), and this was especially pronounced at extensive meadows. This might be explained by the different seasonal patterns of NDVI and PAI, mainly due to large amounts of brown standing biomass.

Higher mean PAI values at extensive compared with intensive meadows for NDVI values lower than 0·9 cannot be fully explained by their higher amount of brown biomass, as the pattern was similar when GAI was compared with NDVI (Figure 3c). Instead, leaf colour might be an important factor. The opposite case in which NDVI values are higher than 0·9 might result from higher maximum GAI reached at intensive meadows.

Usually, the relationship between NDVI and LAI is described as a hyperbolic or exponential function, where NDVI saturates at LAI values around 2 or 3 m^2 m^{-2} (Sellers, 1985; Gamon *et al.*, 1995; Gianelle *et al.*, 2009). For crops, this saturation might be reached at LAI values above 5 m^2 m^{-2} (Viña *et al.*, 2011). A linear relationship is reported for low canopies, for example, Fan *et al.* (2009) and Rocha and Shaver (2009) with LAI <0·8 and <2 respectively. In contrast, some samples in our study had reached maximum NDVI values already at PAI values lower than 1 m^2 m^{-2}. This occurred at intensive meadows, particularly after harvest, if they had been cut before the lower parts of the vegetation had started senescence. The use of spectral indices, which include other wavebands like those in the red-edge (Huete, 1988; Viña *et al.*, 2011), or green spectrum (Gianelle *et al.*, 2009), or a the use of a weighting factor (Gitelson, 2004), might help to overcome the saturation problem, but not the problem of high amounts of brown biomass, which was especially pronounced in extensively managed fen meadows. The resulting high uncertainty has to be considered when using LAI estimated from satellite data, especially for ecosystems that have large amounts of standing litter.

PAI and NDVI as proxies for biomass

Optical measurement methods are important alternatives to destructive biomass sampling and provide a possibility to achieve yield estimates from remote sensing. Large scatter in the relationship between PAI and biomass results from different SPA due to different leaf thicknesses and densities, and different amounts and densities of stems. Unpublished data from leaf area meter (Li-3100; LI-COR) measurements at the studied sites showed considerably higher mean SPA values for plants from intensive (170 cm^2 g^{-1}) meadows compared with plants from extensive meadows (101 cm^2 g^{-1}), where 50% (1st and 3rd quantiles) of the data points ranged between 148 and 202 cm^{-2} g^{-1} (intensive) and 81 and 116 cm^2 g^{-1} (extensive). Species-specific differences ranged from 33 (*Schoenus ferrugineus*) to 204 cm^2 g^{-1} (*Plantago lanceolata*). The higher SPA values for intensive meadows are in accordance with the larger slope of the regression between PAI and dry weight as shown in Figure 4. Based on dependencies between nutrient conditions in plant habitats, relative growth rate and leaf nitrogen, it was postulated that nutrient-rich environments host species with high specific leaf area, whereas species with low specific leaf area are found in nutrient-poor environments (Poorter and De Jong, 1999). Similarly, increasing specific leaf area rates were found with increasing nutrient availability (Meziane and Shipley, 1999). Specific leaf area has further been shown to vary depending on seasonality (Pierce *et al.*, 1994). Additional destructive biomass sampling throughout all seasons for at least 1 year is therefore strongly recommended to identify site-specific correction factors.

In contrast to our results, a strong linear relationship between NDVI and biomass was found in a wetland around a lake in China (Rendong and Jiyuan, 2002). Good correlations have also been reported for wet tundra vegetation (Boelman *et al.*, 2003; Doiron *et al.*, 2013), but their maximum biomass values were much lower than our study. Many studies investigating grasslands on mineral soils have reported a poor relationship between NDVI and biomass (Gamon *et al.*, 1995). To overcome saturation effects at high biomass values, modified indices were introduced which include the blue waveband (Huete *et al.*, 2002) or the near-infrared shoulder (Vescovo *et al.*, 2012), or which are based on narrow bandwidths (Thenkabail *et al.*, 2002) or band depth analysis (Mutanga and Skidmore, 2004). In future research, it would be appropriate to test whether such modified indices can reduce the uncertainty in biomass estimation from satellite data.

NDVI and PAI as proxies for PP

The estimation of PP from NDVI or PAI is of great interest, as more direct photosynthesis measurement methods are cost and effort intensive and they are not feasible on a global scale. Our results showed a management-independent, nearly linear relationship between NDVI and PP. Some studies have reported a strong saturation effect at high rates of photosynthesis when using NDVI based on red and NIR bands (e.g. in a mountain grassland, Gianelle *et al.*, 2009; in a pine forest, Wang *et al.*, 2004) and, therefore, suggest the use of green instead of red wavebands (Gianelle *et al.*, 2009), or additional ones, including blue wavebands (Schubert *et al.*, 2010). Such saturation effects were not distinct in our data and might depend on the ecosystem. A linear relationship between PP and NDVI was supported by findings in tundra (McMichael, 1999), grasslands (Gamon *et al.*, 1995; Wu, 2012) and four northern peatlands (Kross *et al.*, 2013).

GAI was a comparably inferior predictor for PP, due to it being site- and management-dependent and due to saturation at higher GAI values. Saturation between photosynthesis and LAI has been reported by many other studies (Sellers, 1985) and indicates a strong self-shading effect of upper leaves shading lower leaves. In a wet *Senecioni-Brometum* grassland, 50% of the light was found to be intercepted by fewer than 10% of the leaves (Fliervoet and Werger, 1984). Site-specific differences might be explained by different vegetation on the different sites. Species and plant functional type-specific differences in the relationship between LAI and photosynthesis were previously reported for boreal mires (Wilson *et al.*, 2007; Leppälä *et al.*, 2008), ranging from a linear to an exponential relationship. Further uncertainty in the relationship between GAI and PP results from the derivation of GAI from PAI values by applying the poor relationship between green ratio to NDVI. A destructive sampling for a more direct determination of green ratio or GAI was, however, not possible at the chamber plots.

Many ecosystem models use LAI to calculate photosynthesis. Our results showed that NDVI is a better proxy for PP and should therefore be incorporated in carbon models.

Uncertainty in NDVI

Some scatter in the studied relationships could also be caused by uncertainty in the optical measurements. The comparison between NDVI from satellite data and ground measurements was, however, generally in good agreement without bias (data not shown), indicating that the uncertainty in NDVI values is relatively low. With an R^2 of 0·58, the relationship was slightly stronger and showed similar noise compared with the findings of Hmimina *et al.* (2013) for savanna ($R^2 = 0{\cdot}45$) and crops ($R^2 = 0{\cdot}56$) when comparing ground with MODIS NDVI, while they found a R^2 of 0·91 for deciduous forest. Despite using high-resolution (5 m × 5 m) satellite images in our study, the s.e. of 0·08 indicates considerable noise for both intensive and extensive meadows. This can partly be explained by the heterogeneity in the vegetation patches: ground-measured NDVI varied within a vegetation patch each day, on average, by a standard deviation of 0·03 (Table 3). Further uncertainty results from time gaps between ground and satellite measurements. Noise resulting from sensors, sensor angle and elevation, sun angle, background reflection and atmosphere are discussed elsewhere (e.g. Adam *et al.*, 2009 and references therein).

Uncertainty in PAI

When vegetation height and density was low, the PAI probe was not fully covered with vegetation. Therefore, measurement results strongly differ according to the quantity of leaves shading the ceptometer, which depends on solar zenith angle and plant architecture. During spring emergence and especially after harvest, the assumption of a random spherical distribution of leaves might have led to underestimated PAI values. Further, leaf angle and plant architecture can vary considerably between different wet grassland communities (Fliervoet and Werger, 1984). Heterogeneity within the vegetation patches deviated in PAI, on average, by 0·51 $m^2\ m^{-2}$ (Table 3). If tussock sedges were present, the soil surface was especially uneven, which could lead to considerable underestimation of PAI if the probe rested on a high point. The uncertainty resulting from the optical measurement method due to clumping, leaf orientation, plant architecture, leaf size and sun angle (Breda, 2003) is reflected in the noise when ceptometer-based PAI is compared with the more direct method of scanning leaf area (data not shown), which resulted in a rather high s.e. of 1·65 $m^2\ m^{-2}$ and an R^2 value of 0·46.

Conclusions

Almost all investigated relationships differed depending on land-use intensity and they showed large scatter. Thus, for temperate grassland fens, the application of NDVI as a proxy for LAI, biomass or green ratio, as well as PAI and GAI as proxies for biomass or PP, is characterized by high uncertainty and it should be performed under the consideration of the management intensity. This is especially true for less frequently harvested meadows containing high amounts of brown plant material. Optical indices are, however, non-destructive measurement methods that can be automated and are available from satellite images on a global scale. Due to the high uncertainty, it is strongly recommended to perform additional direct measurements of the variable of interest to correct and validate the estimations, especially on extensively managed grasslands and throughout the year. The relationship between NDVI and PP was management independent and showed hardly any saturation effects. Therefore, assimilation models using LAI as an input parameter might consider incorporating NDVI instead.

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