

The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest

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Abstract The creation of gaps can strongly influence forest regeneration and habitat diversity within forest ecosystems. However, the precise characteristics of such effects depend, to a large extent, upon the way in which gaps modify microclimate and soil water content. Hence, the aim of this study was to understand the effects of gap creation and variations in gap size on forest microclimate and soil water content. The study site, in North West England, was a mixed temperate broadleaved deciduous forest dominated by mature sessile oak (*Quercus petraea*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) with some representatives of sycamore (*Acer pseudoplatanus*). Solar radiation (I), air temperature (T_A), soil temperature (T_S), relative humidity (h), wind speed (v) and soil water content (Ψ) were measured at four natural treefall gaps created after a severe storm in 2006 and adjacent sub-canopy sites. I , T_A , T_S , and Ψ increased significantly with gap size; h was consistently lower in gaps than the sub-canopy but did not vary with gap size, while the variability of v could not be explained by the presence or size of gaps. There were systematic diurnal patterns in all microclimate variables in response to gaps, but no such patterns existed for Ψ . These results further our understanding of the abiotic and consequent biotic responses to gaps in broadleaved deciduous forests created by natural treefalls, and provide a useful basis for evaluating the implications of forest management practices.

Keywords Treefall gap · Microclimate · Soil water content · Broadleaved deciduous forest

Introduction

Treefall gaps are a key component of the disturbance regimes in many temperate forests (Peterken 1996; Splechtna et al. 2005) and the importance of gaps for forest regeneration processes has long been recognised (Watt 1925; Platt and Strong 1989). One of the important characteristics of gaps that affects the establishment and growth of tree seedlings is environmental heterogeneity, such as variability in light regimes, within and around gaps (Beatty 1984; Gray and Spies 1996). The structure and vegetation dynamics of temperate forests ecosystems have been investigated in several studies in recent decades (Koop and Hilgen 1987; Emborg et al. 1996; Pontaville et al. 1997; Wolf 2002), and these have led to renewed approaches to forest management and conservation (Bradshaw et al. 1994; Kilian and Fanta 1998). The main emphasis of these alternative management approaches is on natural dynamics and processes in order to obtain stable and self-sustaining forest systems (Attiwill 1994). However, while many studies have focussed on the relationships between forest structure and vegetation dynamics, relatively little attention has been paid to microclimatic conditions (Catherine and Robin 2005; Heithecker and Halpern 2006), owing perhaps to the high cost of making measurements in remote forest sites.

Microclimate is critical to plant species for germination, growth and reproduction; for determining suitable habitat for fauna; and for controlling ecosystem processes such as photosynthesis and nutrient cycling (Jones 1992; Unwin 1997; Gray et al. 2002; Ritter 2005). Microclimate also plays an important role in the ecological processes within

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forests that affect nutrient dynamics and decomposition (Clinton 2003; Ritter et al. 2005). Some aspects of microclimate show strong and predictable relationships with forest structures. For example, solar radiation at the forest floor is directly related to the amount and spatial distribution of canopy cover, as the variations in sky exposure control both net longwave and net shortwave radiation (Drever and Lertzman 2003; Promis et al. 2009). Net all-wave radiation powers micrometeorological processes such as soil heat flux, sensible heat flux, wind and turbulent transport, evapotranspiration and photosynthesis (Kumar et al. 1997) and, therefore, is the main control on climatic differences within the surface-atmosphere boundary layer (De Freitas and Enright 1995). Consequently, many microclimatic variables such as soil and air temperature are controlled by the full vertical profile of vegetation cover (Aussenac 2000; Prevost and Pothier 2003). Other elements of microclimate are less predictable from forest structure. For example, the effects of forest structure on soil moisture may be difficult to determine, as reductions in canopy cover may lead to more evaporation from the soil surface (Morecroft et al. 1998; Chen et al. 1999), but less transpiration loss (Breda et al. 1995).

The creation of a canopy gap by the loss of significant parts of a tree crown, a whole tree or multiple trees represents an extreme and often rapid change in forest structure, with potentially large implications for the microclimate at that locality. The presence of a gap can directly influence the amount of solar radiation, wind patterns and the quantity of precipitation reaching the ground. Differences in these variables have consequences for air temperature, relative humidity, soil temperature and soil moisture content in gaps and under the surrounding sub-canopy (Brown and Whitmore 1992; Carmargo and Kapos 1995; De Freitas and Enright 1995; Mekking and Nijmeijer 1998). It has generally been found that the higher amount of direct solar radiation in a gap leads to an increase in air temperature and soil temperature and a decrease in relative humidity compared to contiguous forest sub-canopy, while the reduced plant uptake of water increases soil water content in gaps (Van Dam 2001; Clinton 2003). However, the observed effects of gap creation on microclimate have tended to lack consistency across studies in different forest types (Collins and Pickett 1987; Riddoch et al. 1991; Brumme 1995; Poulson and Platt 1996; Van Dam 2001; Muscolo et al. 2007). Furthermore, the differences between gap and sub-canopy microclimates can vary diurnally due to the absorption and emission of radiation by vegetation masses. In general, sub-canopy air temperature is lower during the day and higher at night than in gaps (Ghuman and Lal 1987; Chen et al. 1993; Van Dam 2001). However, further evidence is needed concerning the diurnal dynamics of other microclimatic parameters and the effects of gap size on the diurnal differences between sub-canopy and gaps.

It has been acknowledged for some time that, in principle, the microclimatic conditions at the centre of a gap are a function of gap size, shape and orientation, which determine the daily duration of direct insolation (Denslow 1980). Therefore, in general terms, variations in abiotic and biotic conditions depend both on gap size and within-gap position (Nakashizuka 1985; Vitousek and Denslow 1986; Collins and Pickett 1987, 1988; Platt and Strong 1989; Runkle 1989; Holeksa 2003; Kwit and Platt 2003). Rose (2000) found that the growth performance of vegetation species increases with increasing gap size, if light, water or nutrients are the only limiting variables. Seedling and sapling growth is influenced by the changes in microclimatic conditions such as solar radiation, temperature and changes in water and nutrient availability (Welden et al. 1991). Thus, understanding forest regeneration in gaps requires a thorough knowledge of microclimatic conditions in relation to gap size (Rose 2000; Van Dam 2001). While work such as that of Ritter (2005) has found that microclimate changes in small gaps are less pronounced than in large gaps, information remains scarce on exactly how gap size affects the microclimate and soil water balance. Indeed, because of the contradictory results from gap studies in different forest types it is difficult to make generalisations, and a wider range of case studies is necessary to enhance our understanding of the effects of gap size on microclimate and soil moisture variations (Gray et al. 2002; Ritter et al. 2005). Within temperate forests, there have been several recent and very informative studies but these have had slightly different foci and approaches, such as examining the effect of gap size by studying artificially created gaps in coniferous and broad-leaved deciduous forest (e.g. Gahidy et al. 2006; Muscolo et al. 2007) and understanding the effects of gap creation by studying the spatio-temporal variations in microclimate within a single natural gap (Ritter et al. 2005). In order to build upon these recent studies, the present work focussed on a number of recently naturally created gaps of a range of sizes in a temperate broadleaved deciduous forest. The objective of this study was to analyse the effects of gap creation and variations in gap size on solar radiation, air temperature, soil temperature, relative humidity, wind speed and soil water content, in terms of their overall characteristics and diurnal patterns.

Methods

Study area and experimental design

The investigation was carried out in Eaves Wood located in the north of the county of Lancashire in England (2°49'W, 54°10'N). Eaves Wood is situated within the designated

Arnside and Silverdale Area of Outstanding Natural Beauty (AONB) and it is a Site of Special Scientific Interest (SSSI) notified under the Wildlife and Countryside Act, 1981. It covers an area of 51.5 ha and is owned and managed by the National Trust. The climate is maritime temperate with a growing season of 7 months (April–October). Eaves Wood is a mixed semi-natural deciduous forest that is largely secondary in nature but there is evidence that it has not been completely cleared, historically. There is a wide diversity of species, including many rare and uncommon herbaceous plants, over 250 species of fungi and a variety of animal life including the insect *Issus muscaeformis* and the brown snail (*Zenobiella subrufescens*), which is distributed quite widely in western Britain but usually associated with primary forest. Hazel (*Corylus avellana*) is commonly found forming an understorey along with a wide variety of shrubs and woody species, including the wild service tree (*Sorbus torminalis*) and the very rare Lancaster white beam (*Sorbus lancastriensis*), most of which regenerate freely within Eaves Wood. The area used for this study was dominated by mature sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*), with sub-dominants being sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*). The stand structure is heterogeneous with trees of different size-classes, canopy gaps (covering 8% of the forest area) and regeneration patches.

For the purposes of this study, four naturally created gaps were selected that covered the range of sizes typical of naturally formed gaps within this forest. Table 1 shows the attributes of the chosen gaps. A gap was defined as a canopy opening created by the windthrow and death of at least one mature tree. The smallest gap had a near-circular shape while the other gaps were more irregular in shape. The experimental gaps were positioned at sites with similar aspect, slope, topography, shape and surrounding canopy properties. All of the gaps were created by single or multiple treefalls caused by a severe storm in December 2006. The requirement to use gaps

with similar characteristics and origin somewhat restricted the total number of gaps that could be sampled in the experiment. Further, there are inevitable logistical and financial limitations of the intensive field measurements required for this type of study. Indeed, this has been recognised previously by de Freitas and Enright (1995), who were constrained to sampling two gaps over 4 days in order to characterise the effect of gap size on microclimate. Within the four gaps used in this experiment, none of the wind thrown trees had been removed from the gaps due to the protected status of the forest. As the gaps had been created by fallen mature trees, which tend to preclude the development of lower canopy strata in these forests, there was little understorey present within any of the gaps at the time of the study. Regeneration had only just begun, with seedlings a few centimetres in height occupying small areas of some of the gaps. A total station was used to measure the area (hereafter referred to as gap size) of each gap and to identify the positions of the centres of the gaps, where micrometeorological measurements were made. Gap size ranged from 40 to 286 m² and the height of the surrounding tree canopy was approximately 25 m at all sites.

Each gap site was paired with a site beneath the canopy located 30 m from the southern edge of the gap. At the eight sites (four pairs of gap and sub-canopy sites), micrometeorological measurements were made between 24 July and 26 September 2007, covering the period of maximum leaf canopy development when we might expect the microclimatic affects of gaps to be most extreme. Ten-minute averages of data from a 5 sec sampling interval were logged for the following variables: solar irradiation (I) was measured using Kipp & Zonen's CMP3 pyranometers, which have a thermopile sensor with a flat 300–3,000 nm spectral sensitivity. Wind speed (v) was measured with A100R 3-cup anemometers (Campbell Scientific, Logan, UT). The pyranometers and anemometers were mounted on a mast at 2 m above ground level. Air temperature (T_A) and relative humidity

Table 1 Physical and historical characteristics of four naturally created gaps (1, 2, 3, 4) of the Eaves Wood forest

Variable	1	2	3	4
Area (m ²)	40	150	210	286
Perimeters (m)	33	75	90	97
Ratio area/perimeter	1.21	2.00	2.33	2.95
Canopy openness (%) (gaps & adjacent sub-canopy)	10.2(3.5)	25.4(4.4)	30.5(4.5)	43.5(7.3)
Aspect	South	South West	South	Flat
Elevation (m)	69.4	69.6	69.4	69.8
Mean slope (%)	2.1	8.1	2.6	2.0
Former stand	Quercus	Fagus	Fagus	Fagus
Surrounding stand	Quercus	Fagus, Quercus	Fagus, Quercus	Fagus, Quercus

(*h*) were measured using combined air temperature and relative humidity sensors model HMP50 (Campbell Scientific), which were surrounded by radiation shields and mounted at 1.8 m above ground level. Soil temperature (T_S) was measured with sensor models ARG107 (Campbell Scientific) and ST1 (Delta-T Devices, Cambridge, UK) placed at 5 cm depth (Ritter et al. 2005) from the top of the mineral soil. Volumetric soil water content (Ψ) of the upper 5 cm of soil was measured using theta probes model ML2x (Delta-T Devices). The theta probes consisted of a waterproof housing that contains the electronics and attached to it four sharpened stainless steel rods that were inserted vertically into the soil.

At each gap and sub-canopy site canopy openness was estimated using the gap fraction values provided by an LAI-2000 plant canopy analyser (hemispherical sensor; Stenberg et al. 1999). These data indicated the fraction of the sky that is not blocked by the foliage, branches, or trunks, with values ranging between 0 (no sky visible to the sensor) and 1 (unobscured sky).

Statistical analysis

Effects of gap size and sub-canopy on microclimates and soil water content were analysed by calculating the mean and maximum daily values of solar irradiation ($I_{\text{mean,max}}$), air temperature ($T_{A,\text{mean,max}}$), soil temperature ($T_{S,\text{mean,max}}$), soil water content ($\Psi_{\text{mean,max}}$), relative humidity ($h_{\text{mean,max}}$) and wind speed ($v_{\text{mean,max}}$) collected over the 24-h periods. These mean and maximum daily values were used for the statistical analysis.

To examine the variability of microclimates and soil moisture in gaps of different sizes and beneath the forest canopy, one way ANOVA tests were applied to the data for I , T_A , T_S , Ψ , h and v for gaps and sub-canopy. Assumptions of normality and homogeneity were checked and found to be valid. The correlation between T_A and T_S were tested by calculating Pearson correlation. The factor day had two levels: clear-skies and overcast. Clear-skies days had cloudless conditions while overcast days had full cloud cover and these days were chosen to represent the extremes of daily solar radiation levels over the sampling

period. Fourteen days with each of these conditions were chosen for the analysis, based on cloud factor data obtained from a nearby automatic weather station. All statistical tests were conducted in SPSS software (SPSS Version 15, Chicago, IL), the significance level was $P < 0.05$.

Results

Solar radiation

There was a significant effect of gap size on I_{mean} throughout the measurement period ($P < 0.05$), and I_{mean} was significantly higher ($P < 0.05$) in gaps than the sub-canopy (Table 2). Figure 1a demonstrates a similar pattern for I_{max} , where there was a significant effect of gap size ($P < 0.05$), with the largest gap receiving 638 W m^{-2} and the smallest gap 90.1 W m^{-2} . I_{max} in gaps was significantly higher ($P < 0.05$) than in the sub-canopy overall. Concerning the diurnal patterns of radiation (Fig. 2), on clear-skies days the largest gap experienced rapid changes in radiation while the smaller gaps and sub-canopy had much smoother changes in radiation. In this and subsequent figures, mean values representing sub-canopy conditions are plotted (for simplification), as there were no significant differences ($P > 0.05$) between the four sub-canopy sites for all microclimate variables. As can be seen in Fig. 2, on overcast days, radiation was lower than clear-skies days for all gaps and the sub-canopy, with generally a smoother change throughout the day on overcast days.

Air temperature

The $T_{A,\text{max}}$ observed at the centre of the gaps was significantly different ($P < 0.05$) between gaps of different sizes, as can be observed in Fig. 1b. Over the measurement period, $T_{A,\text{max}}$ ranged between an average of 21.6°C in the largest gap and 16.7°C in the smallest gap. $T_{A,\text{max}}$ at the centre of gaps was significantly higher ($P < 0.05$) than the sub-canopy. However, the $T_{A,\text{mean}}$ did not vary

Table 2 Values of mean daily solar irradiation (I), air temperature (T_A), soil temperature (T_S), wind speed (v) and relative humidity (h) in the gaps and the sub-canopy, averaged throughout the measurement period (mean \pm standard error)

Variable	Sub-canopy	Gap 1 (40m ²)	Gap 2 (150m ²)	Gap 3 (210m ²)	Gap 4 (286m ²)
I_{mean} (W m ⁻²)	7 \pm 12*	13 \pm 19*	29 \pm 38*	30 \pm 39	92 \pm 150*
$T_{A,\text{mean}}$ (°C)	14.8 \pm 2.8*	14.7 \pm 1.4*	14.3 \pm 1.9*	15.1 \pm 1.4*	14.9 \pm 3.0*
$T_{S,\text{mean}}$ (°C)	13.3 \pm 0.4*	13.6 \pm 0.4*	13.8 \pm 0.5*	13.9 \pm 0.5*	15.6 \pm 1.4*
Ψ_{mean} (%)	12.8 \pm 1.5*	16.4 \pm 3.1*	33.7 \pm 1.6*	40.4 \pm 5.3*	49.5 \pm 5.4*
h_{mean} (%)	92.1 \pm 7.9	87.3 \pm 8.5	83.2 \pm 9.6	86.9 \pm 9.7	81.8 \pm 12.8
v_{mean} (m s ⁻¹)	0.4 \pm 0.3	0.5 \pm 0.1	0.3 \pm 0.1	0.4 \pm 0.1	0.3 \pm 0.1

*Significantly different ($P < 0.05$)

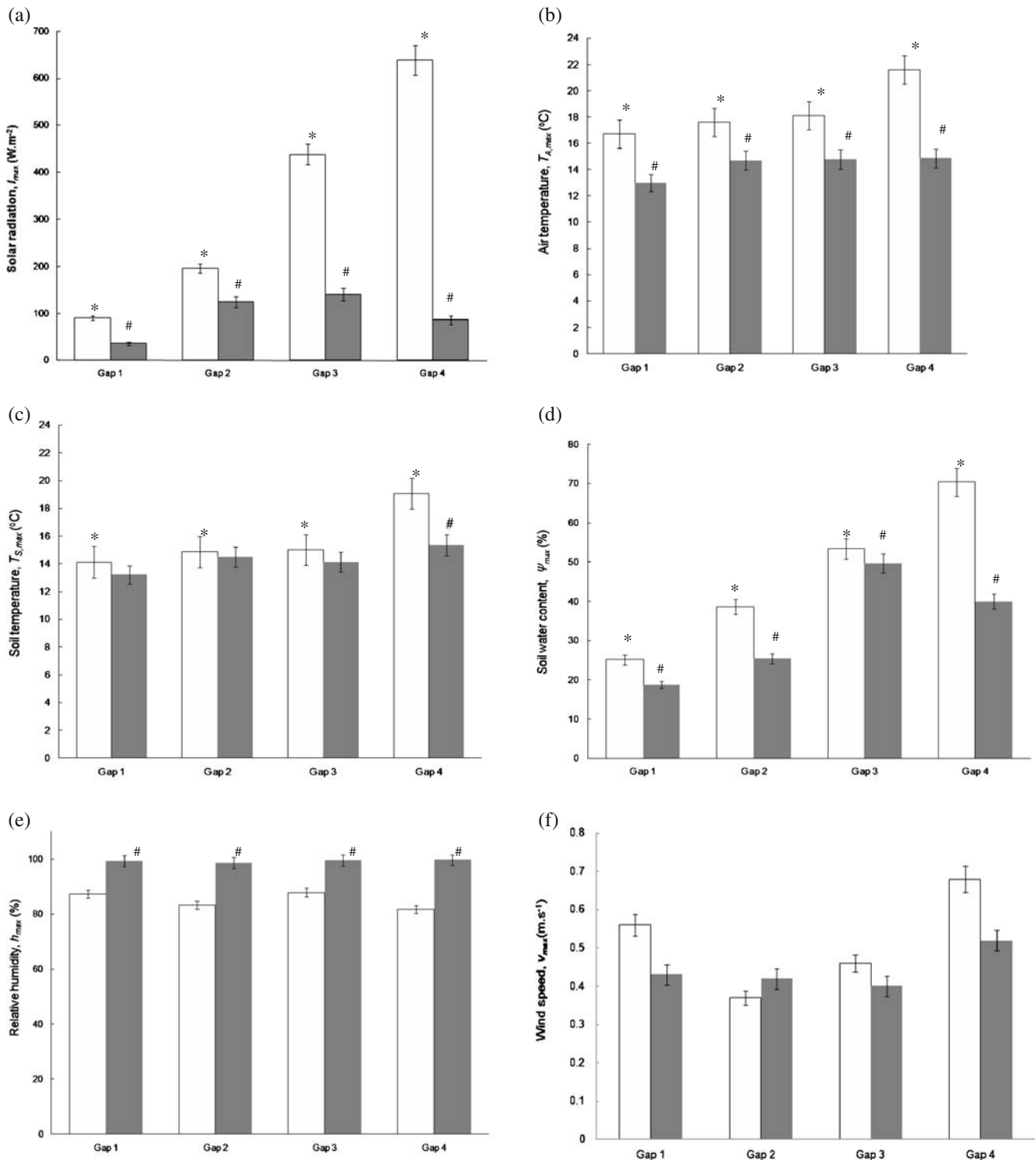


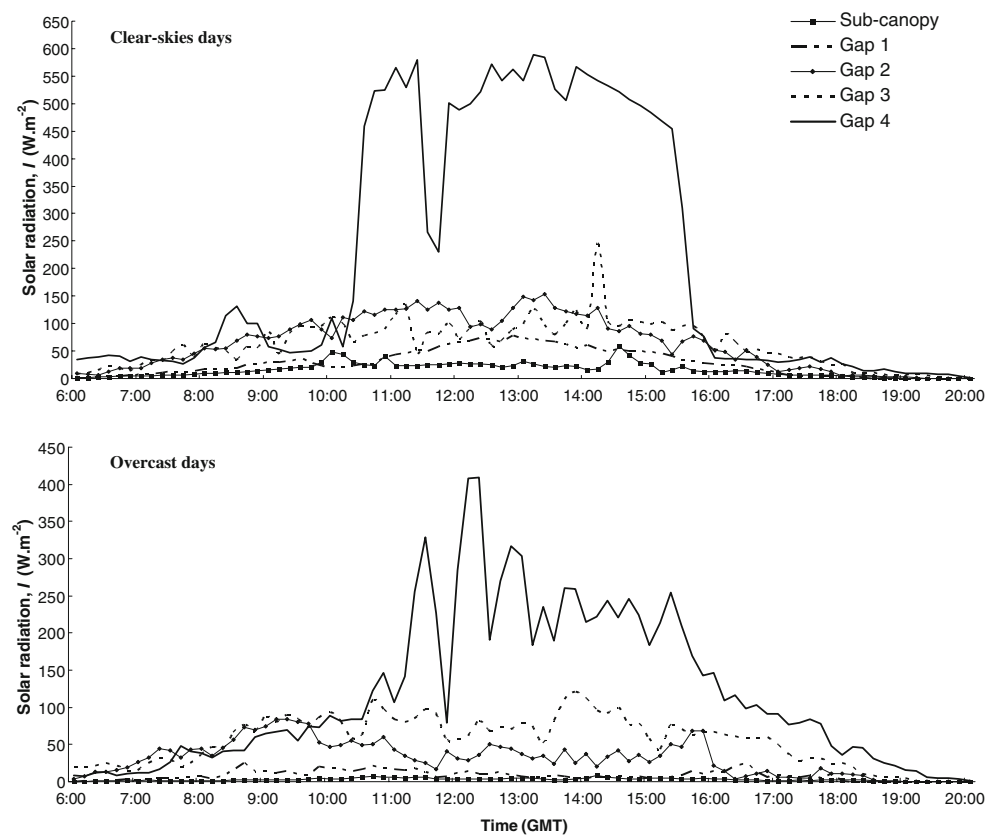
Fig. 1 Values of maximum daily (a) solar radiation, I_{max} ; (b) air temperature, $T_{A,max}$; (c) soil temperature, $T_{S,max}$; (d) soil water content, ψ_{max} ; (e) relative humidity, h_{max} ; and (f) wind speed, v_{max} measured

within gaps and adjacent sub-canopies (in grey) is averaged over the measurement period. Bars Standard error. * Significant differences between gaps, # significant differences between gap and sub-canopy

significantly with gap size and gaps were not significantly different to sub-canopy temperatures (Table 2). Concerning diurnal variations, Fig. 3 demonstrates that the gaps generally had a greater range of T_A variation than the sub-

canopy, and that diurnal range increased with gap size. T_A was consistently higher in gaps than in the sub-canopy during day time but gaps have similar or lower temperatures than the sub-canopy during night time.

Fig. 2 Diurnal patterns of solar radiation, I for gaps and sub-canopy on clear-skies and overcast days. Four days of data were averaged for each of these plots



Soil temperature

As shown in Fig. 1c and Table 2, there were significant differences ($P < 0.05$) in $T_{S,max}$ and $T_{S,mean}$ between gaps of different sizes throughout the measurement period. The largest gap had the highest $T_{S,max}$ (19.1°C) and the smallest gap the lowest $T_{S,max}$ (14.1°C), with a 4°C to

5°C difference being typical at midday. $T_{S,max}$ and $T_{S,mean}$ were higher at the centre of gaps than in the sub-canopy throughout the measurement period but the differences were significant ($P < 0.05$) only for the largest gap. The plot of diurnal variations (Fig. 4) demonstrates that T_S was consistently higher in gaps than in the sub-canopy during day and night. The diurnal range of T_S increased with gap

Fig. 3 Diurnal variations of air temperature, T_A for the gaps and the sub-canopy, averaged over the measurement period

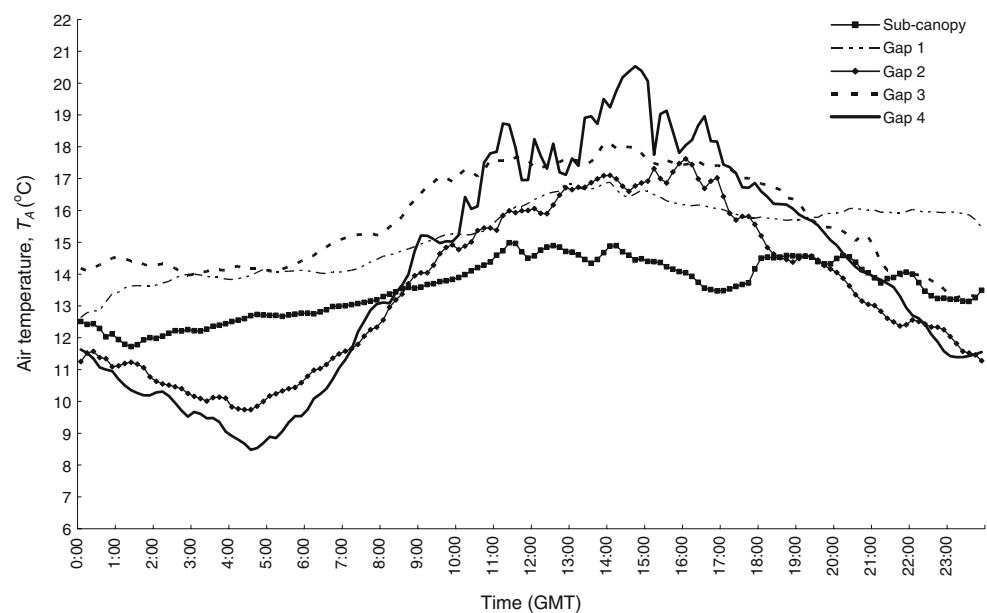
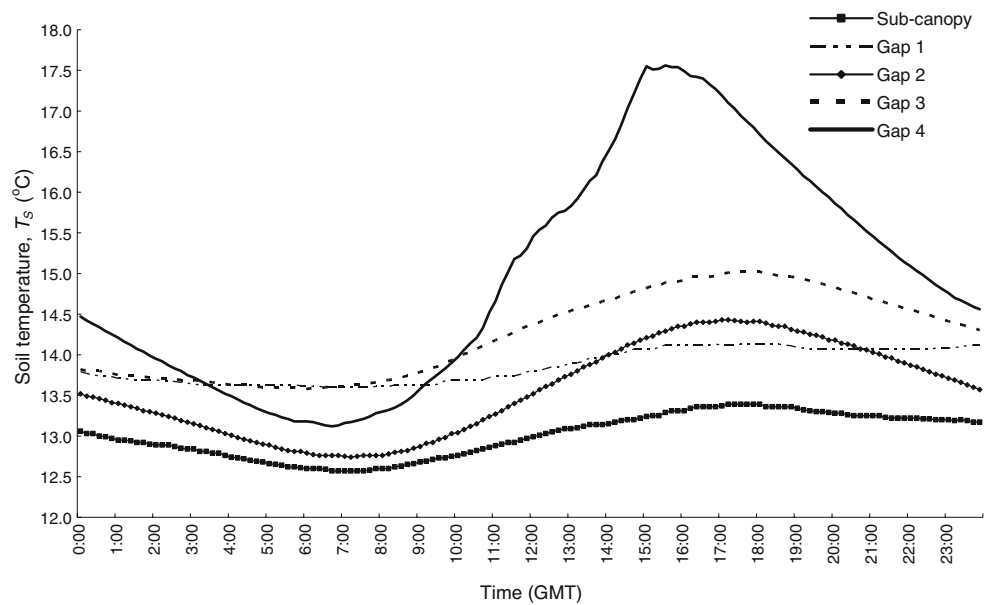


Fig. 4 Diurnal variations in T_s for the gaps and the sub-canopy, averaged over the measurement period



size, with the larger gaps showing a greater warming during the daytime and greater cooling at night. Interestingly, T_s in the largest gap reached its maximum diurnal temperature some time before this was reached in the other gaps and sub-canopy. There were slightly greater differences in soil temperature than air temperature across gaps of different sizes, but a similar pattern was evident. There was some correlation between soil temperature and air temperature ($R=0.55$, $P<0.01$), but mean daily soil temperature was between 1 and 5°C lower than air temperature throughout the measurement period.

Soil water content

A significant effect of gap size ($P<0.05$) was found on Ψ_{mean} throughout the measurement period (Table 2). Similarly, Ψ_{max} increased with gap size, as is shown in Fig. 1d, where Ψ_{max} ranged between 25.1% for the smallest gap to 70.4% for the largest. The soils within gaps were consistently more moist, both in terms of Ψ_{mean} and Ψ_{max} , than the sub-canopy ($P<0.05$). There were no systematic diurnal patterns in Ψ either within gaps or the sub-canopy.

Relative humidity

As Table 2 shows, there were no systematic changes in h_{mean} with gap size, but h_{mean} within gaps was consistently lower than the sub-canopy; however, a high variability meant that the differences in h_{mean} were not statistically significant. Similarly, h_{max} showed no significant changes with gap size, with only a small variation between the

largest gap and smallest gap, with h_{max} values of 81.8% and 87.3%, respectively (Fig. 1e). However, the data do show that h_{max} in the gaps was significantly lower than in the sub-canopy ($P<0.05$).

Wind speed

Variations in both v_{mean} and v_{max} were independent of gap size, and there was no significant difference between the gaps and the sub-canopy for either parameter (Table 2, Fig. 1f). However, v was significantly higher ($P<0.05$) during the day time than night time in all gaps and in the sub-canopy (Fig. 5). There is some indication that the difference between day and night time values of v increased with gap size, as the smallest gap showed a day–night

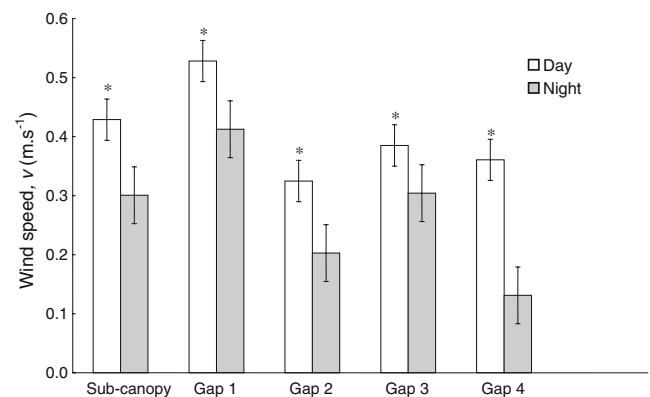


Fig. 5 Day time and night time wind speed, v in gaps and the sub-canopy, averaged over the measurement period. Bars Standard error. * Significant differences between day time and night time

difference of 0.12 m s^{-1} while the largest gap had a difference of 0.23 m s^{-1} .

Discussion

Previous studies in temperate forests found that microclimate conditions such as solar radiation, air and soil temperature and soil moisture were directly influenced by the formation of gaps (Collins and Pickett 1988; Canham et al. 1990; Galhidy et al. 2006) and gap size (De Freitas and Enright 1995; Gagnon et al. 2004; Bouchard et al. 2005; Heithecker and Halpern 2006). Our results support these findings.

Solar radiation was significantly higher in gaps than in the sub-canopy throughout the measurement period regardless of sky conditions (clear-skies or overcast days) and increased significantly with gap size. Our results are in agreement with the study by De Freitas and Enright (1995), where mean daytime solar radiation levels increased from 164 W m^{-2} at the centre of a small gap to 452 W m^{-2} in a large gap. There were rapid diurnal changes in radiation in the largest gap on clear-skies days, whereas the smaller gaps experienced smoother changes in radiation levels. These findings can probably be attributed to the greater proportion of direct radiation reaching the centre of the large gap, whereas, in smaller gaps, solar radiation was predominantly diffuse or being transmitted through the canopy edge, leading to more gradual and less extreme changes in radiation levels. Similar findings were reported by Ritter et al. (2005) in a semi-natural deciduous forest in Denmark. Our results also demonstrated that on overcast days, while solar radiation was lower for all gaps and sub-canopy, there was a smoother change throughout the day in radiation levels than on clear-skies days. Interestingly, in the early morning and late afternoon on overcast days, solar radiation in gaps was generally higher than at that time on clear-skies days. This could be due to the effect of clouds diffusing radiation into gaps at these times, which was not the case on clear-skies days.

Evidently, the higher solar radiation levels in gaps contributed to higher air and soil temperatures. This accords with mechanisms whereby sky exposure controls net allwave radiation and sensible and latent heat fluxes as discussed by De Freitas and Enright (1995). Based on the present results, air temperature in gaps was influenced directly by the amount and duration of solar radiation received. Previous work has also found that the air temperature responses to gap creation were associated closely with direct radiation (Gray et al. 2002). Similarly, a close correlation between soil temperature and solar radiation was also reported in a study by Balisky and Burton (1993). The correlation between soil and air temperature found in the present study accords with

previous work by Ritter et al. (2005), who also found that soil and air temperatures were higher within gaps than in the sub-canopy. Our observations that the largest gap experienced a rapid rate of soil warming may result from the larger proportion of direct solar radiation impinging on the soil surface. In the smaller gaps and sub-canopy, soil heating may be taking place at a slower rate in response to a greater proportion of diffuse solar radiation and thermal emission of surrounding vegetation, as found by Van Dam (2001). Furthermore, our results demonstrated that, throughout the diurnal cycle, gap soils consistently had a higher temperature than sub-canopy soils, whereas air temperature within gaps was higher than the sub-canopy during the day time but lower at night time. It is likely that these differences can be explained by the greater thermal inertia of soils compared to air (Melesse 2004).

Our results show that soil water content was higher in gaps than in the sub-canopy and increased with gap size, in accordance with findings in other temperate deciduous forests (Geiger et al. 1995; Ritter et al. 2005; Galhidy et al. 2006), boreal coniferous forests (Gray et al. 2002) and moist tropical forests (Veenendaal et al. 1995). This has been attributed to the combined effects of an increase in precipitation reaching the soil because of reduced canopy interception and storage, and a decrease in transpiration in the gap due to reduced active vegetation (Zirlewangen and von Wilpert 2001; Zhu et al. 2003). Conversely, water extraction by trees is expected to decrease the water content of the sub-canopy soils (Muller and Wagner 2003). However, a study by Arunachalam and Arunachalam (2000) found that canopy gaps had lower soil water content than the sub-canopy in a sub-tropical humid forest of north-east India. This could possibly be explained by (1) a lack of difference in precipitation reaching the soil within gaps and the sub-canopy, in a region with high and intense rainfall; (2) the higher radiation receipt and higher soil temperatures within gaps leading to high rates of evaporation that possibly counteract any reduction in transpiration; or (3) a significant component of understorey vegetation remaining within gaps (despite the loss of a dominant tree), which is capable of high rates of transpiration within the higher air temperature environment of the gap. It appears then, that the extent to which gap creation affects soil water content and whether there is an increase or decrease relative to the sub-canopy, is likely to be controlled by the relative magnitude of conditions that may lead to an increase in water supply to the soil in the gap and those that effect water loss. This suggests that further work is needed to fully characterise this complex set of interactions that control soil water content, in forests of different types in different environmental settings.

Relative humidity was consistently lower in gaps than in the sub-canopy, which is the inverse of the pattern observed for other microclimate variables. In particular, maximum daily

relative humidity (h_{\max}) in the gaps was significantly lower than in the sub-canopy. This may be explained by (1) the reduced leaf area of transpiring vegetation within the gap as opposed to the sub-canopy sites, which are effectively enveloped in a large leaf area; or (2) the increased propensity for mixing of the air within gaps with less humid atmosphere outside of the forest, compared with the sub-canopy atmosphere, which is constrained beneath the tree layer. Thus, during periods of peak evapotranspiration, h_{\max} is lower in gaps compared to the sub-canopy as discussed by Nielsen and Mackenthun (1991) and Ritter et al. (2005).

The lack of any differences between gap and sub-canopy wind speeds was interesting and appears to conflict with previous findings that suggest that gaps can create turbulence that may damage surrounding trees, especially where very dense stands are concerned (Aussenac 2000). Within the study site used, the paucity of the understorey and therefore the lack of barriers to air movement within the sub-canopy, combined with the presence of large trunks and branches of windthrown trees that remained in all of the gaps studied, may explain the similarities between gap and sub-canopy windspeeds. Our results indicated that wind speed tended to be strongest during daylight hours within gaps and the sub-canopy, peaking between noon and late afternoon (between 1200 and 1600 hours). Other studies have also found higher windspeeds within forests during the daytime than at night (Morecroft et al. 1998). This may result from convective forces induced by solar radiation within gaps leading to air mixing between gaps and sub-canopy and thus higher daytime windspeeds (Scharenbroch and Bockheim 2007). The increase in the difference between day and night-time windspeeds with gap size, corresponds to an increase in solar radiation and maximum daily air and soil temperature with gap size, and this appears to support the idea of radiation-induced convective forces developing within gaps and increasing with gap size. Such diurnal differences in wind speed have a number of implications, for example, in creating different microhabitat conditions, temporally. Faunal species that have specific diurnal behavioural patterns may use different components of the forest canopy and gap mosaic for different activities, such as foraging and roosting, at different times during the diurnal cycle. Consequently, the link between gap spatial properties and microclimate temporal properties may have important implications for habitat and species diversity within forests.

Conclusion

In this temperate broadleaved deciduous forest, gap size has a strong influence on some of the microclimate variables investigated. As expected, solar radiation, air temperature, soil

temperature and soil water content increased significantly with gap size. The diurnal patterns of solar radiation within gaps varied considerably between overcast and clear-skies conditions, while soil temperature in gaps was consistently higher than in the sub-canopy, whereas air temperature within gaps was higher than the sub-canopy during the day time but lower at night time. However, relative humidity was consistently lower in gaps than in the sub-canopy but did not vary with gap size. We suggest that variations in wind speed could not be explained by the presence or size of gaps and that this variable appears to have a more complex response to forest structure than the other microclimatic variables. However, there were systematic diurnal variations in wind speed and the difference between day and night time wind speed increased with gap size.

This study has provided some useful evidence concerning the effects of gap size on microclimates and soil water balance in a temperate broadleaved deciduous forest, and this knowledge is valuable for assessing the implications of gap creation for forest ecosystem functioning and regeneration. In particular, combining our findings with measures of the size and spatial distribution of gaps within forests, e.g. as monitored using remote sensing techniques (e.g. Koukoulas and Blackburn 2004, 2005), will enable us to construct a comprehensive understanding of the spatial and temporal dynamics of microclimates across entire forest stands. Such approaches should allow us to assess the implications for forests in terms of abiotic dynamics and consequently the biotic response following the creation of natural or anthropogenic gaps. This will more fully inform management decisions regarding the creation of new gaps through tree removal or coppicing and the maintenance of gaps using practices such as conservation grazing, to create habitat diversity and promote regeneration. Such management practices are increasingly being undertaken in temperate forests. There is considerable potential for linking approaches based on field data, modelling and remote sensing techniques in order to contribute to the development of management strategies, and this will be the focus of our future work.

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References

- Arunachalam A, Arunachalam K (2000) Influence of gap size and soil properties on microbial biomass in a subtropical humid forest of north-east India. *Plant Soil* 223:185–193

- Attiwill PM (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. *For Ecol Manag* 63:247–300
- Aussenac G (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann For Sci* 57:287–301
- Balisky AC, Burton PJ (1993) Distinction of soil thermal regimes under various experimental vegetation covers. *Can J Soil Sci* 73:411–420
- Beatty SW (1984) Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* 65:1406–1419
- Bouchard M, Kneeshaw D, Bergeron Y (2005) Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. *For Ecol Manag* 204:297–313
- Bradshaw R, Gemmel P, Björkmann L (1994) Development of nature-based silvicultural models in southern Sweden: the scientific background. *For Landsc Res* 1:95–110
- Breda N, Granier A, Aussenac G (1995) Effects of thinning on soil water balance and tree water relations, transpiration and growth in oak forest (*Quercus petraea* (Matt) Liebl.). *Tree Physiol* 15:295–306
- Brown ND, Whitmore TC (1992) Do dipterocarp seedlings really partition tropical rain forest gaps? *Philos Trans R Soc Lond B* 335(1275):369–378
- Brumme R (1995) Mechanisms of carbon and nutrient release and retention in beech forest gaps. *Plant Soil* 168–169:579–584
- Canham CD, Denslow JD, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and treefall gaps in temperate and tropical forests. *Can J For Res* 20:620–631
- Carmargo JLC, Kapos V (1995) Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J Trop Ecol* 11(2):205–220
- Catherine LC, Robin LC (2005) Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica* 37(2):238–244
- Chen J, Franklin JF, Spies TA (1993) Contrasting microclimates among clear cut, edge, and interior of old-growth Douglas-fir forest. *Agric For Meteorol* 63:219–237
- Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL, Franklin JF (1999) Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288–297
- Clinton BD (2003) Light, temperature and soil moisture response to elevation, evergreen understorey, and small canopy gaps in the southern Appalachians. *For Ecol Manag* 186:243–255
- Collins BS, Pickett STA (1987) Influence of canopy opening on the environment and herb-layer in a northern hardwoods forest. *Vegetatio* 70:3–10
- Collins BS, Pickett STA (1988) Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J Ecol* 76:437–450
- De Freitas CR, Enright NJ (1995) Microclimatic differences between and within canopy gaps in a temperate forest. *Int J Biometeorol* 38:188–193
- Denslow JS (1980) Gap partitioning among tropical rainforest trees. *Biotropica* 12(2):47–55
- Drever RC, Lertzman KP (2003) Effects of a wide gradient of retained tree structure on understorey light in coastal Douglas-fir forests. *Can J For Res* 33:137–146
- Emborg J, Christensen M, Heilmann-Clausen J (1996) The structure of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For Landsc Res* 1:311–333
- Gagnon JL, Jokela EJ, Huber DA (2004) Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems. *For Ecol Manag* 187:373–380
- Galhidy L, Mihok B, Hagyo A, Standovair RT (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of Hungarian beech forest. *Plant Ecol* 183:133–145
- Geiger R, Aran RH, Todhunter P (1995) *The climate near ground*, 5th edn. Vieweg, Wiesbaden
- Ghuman BS, Lal R (1987) Effects of partial clearing on microclimate in a humid tropical rainforest. *Agric For Meteorol* 40:17–29
- Gray AN, Spies TA (1996) Gap size, within gap position and canopy structure effects on conifer seedling establishment. *J Ecol* 84:635–645
- Gray AN, Spies TA, Easter MJ (2002) Microclimate and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can J For Res* 32:332–343
- Heithecker TD, Halpern CB (2006) Variation microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. *For Ecol Manag* 226:60–71
- Holeksa J (2003) Relationship between field-layer vegetation and canopy openings in a carpathian subalpine spruce forest. *Plant Ecol* 168:57–67
- Jones HG (1992) *Plants and microclimate: a quantitative approach to plant physiology*. Cambridge University Press, Cambridge
- Kilian W, Fanta J (1998) Degradation of forest site and possibilities for their recovery. *Ecol Eng* 10:1–3
- Koop H, Hilgen P (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica* L.) stands at Fontaine Bleu (France). *For Ecol Manag* 20:135–150
- Koukoulas S, Blackburn GA (2004) Quantifying the spatial properties of forest canopy gaps using LiDAR imagery and GIS. *Int J Remote Sens* 25:3049–3071
- Koukoulas S, Blackburn GA (2005) Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. *J Veg Sci* 16:587–596
- Kumar L, Skidmore AK, Knowles E (1997) Modelling topographic variation in solar radiation in GIS environment. *Int J Geogr Inf Sci* 11(5):475–497
- Kwit C, Platt WJ (2003) Disturbance history influences regeneration of non-pioneer understorey trees. *Ecology* 84:2575–2581
- Mekkink MJ, Nijmeijer RG (1998) Microclimatological and hydrological ecosystem components within man-made gaps in tropical rain forest of Guyana. Tropenbos-Guyana Programme, Georgetown, Guyana. Dissertation, Utrecht University, The Netherlands
- Melesse AM (2004) Spatiotemporal dynamics of land surface parameters in the Red River of the North Basin. *Phys Chem Earth* 29:795–810
- Morecroft MD, Taylor ME, Oliver HR (1998) Air and soil microclimates of deciduous woodland compared to an open site. *Agric For Meteorol* 90:141–156
- Muller KH, Wagner S (2003) Fine root dynamics in gaps of Norway spruce stands in the German Ore Mountains. *Forestry* 76:149–158
- Muscolo A, Sidari M, Mercurio R (2007) Variations in soil chemical properties and microbial biomass in artificial gaps in silver fir stands. *Eur J For Res* 126:59–65
- Nakashizuka T (1985) Diffused light conditions in canopy gaps in a beech (*Fagus crenata* Blume) forest. *Oecologia* 66:472–474
- Nielsen CHN, Mackenthun G (1991) Die horizontale Variation der Feinwurzelintensität in Waldböden in Abhängigkeit von der Bestockungsdichte. *Allg Forst-Jagdztg* 162:112–119
- Peterken GF (1996) *Natural woodland*. Cambridge University Press, Cambridge
- Platt WJ, Strong DR (1989) Gaps in forest ecology. *Ecology* 70(3):535–535
- Pontailier JY, Faille A, Lemée G (1997) Storms drive successional dynamics in natural forest: a case study in forest (France). *For Ecol Manag* 98:1–15
- Poulson TL, Platt WJ (1996) Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77:1234–1253

- Prevost M, Pothier D (2003) Partial cuts in a trembling aspen-conifer stand: effects on micro environmental conditions and regeneration dynamics. *Can J For Res* 33:1–15
- Promis A, Schindler D, Reif A, Cruz G (2009) Solar radiation transmission in and around canopy gaps in an uneven-aged *Nothofagus betuloides* forest. *Int J Biometeorol*. doi:10.1007/s0048400902227
- Riddoch I, Lehto T, Grace J (1991) Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytol* 119:137–147
- Ritter E (2005) Litter decomposition and nitrogen mineralization in newly formed gaps in a Danish beech (*Fagus sylvatica*) forest. *Soil Biol Biochem* 37:1237–1247
- Ritter E, Dalsgaard L, Einhorn KS (2005) Light, temperature and soil moisture regimes following gap formation in a semi-natural beech dominated forest in Denmark. *For Ecol Manag* 206:15–33
- Rose SA (2000) Seeds, seedlings and gaps—size matters. A study in the tropical rain forest of Guyana. Dissertation, Utrecht University, The Netherlands
- Runkle JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70:553–555
- Scharenbroch BC, Bockheim JG (2007) Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant Soil* 294:219–233
- Splechtna BE, Gratzner G, Black BA (2005) Disturbance history of a European old-growth mixed-species forest—a spatial dendro-ecological analysis. *J Veg Sci* 16:511–522
- Stenberg P, Kangas T, Smolander H, Linder S (1999) Shoot structure, canopy openness, and light interception in Norway spruce. *Plant Cell Environ* 22:1133–1142
- Unwin DJ (1997) *Microclimate measurement for ecologists*. Academic, London
- Van Dam O (2001) *Forest filled with gaps. Effects of gap size on water and nutrient cycling in tropical rain forest. A study in Guyana*. Dissertation, Utrecht University, The Netherlands
- Veenendaal EM, Swaine VK, Agyeman DB, Abebresse IK, Mullins CE (1995) Differences in plant and soil water relations in and around gap in West Africa during the dry season may influence seedling establishment and survival. *J Ecol* 83:83–90
- Vitousek PM, Denslow JS (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J Ecol* 74:1167–1178
- Watt AS (1925) On the ecology of British beechwoods with special reference to their regeneration: part II, section II and III. The development and structure beech communities on the Sussex Downs. *J Ecol* 13:27–33
- Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) Sapling survival, growth and seedling establishment: relationship to canopy height in a neotropical forest. *Ecology* 72:35–50
- Wolf A (2002) *Tree dynamics in Draved Forest: a long-term study of a temperate deciduous forest in Denmark*. Dissertation. Geological Survey of Denmark and Greenland & The Royal Veterinary and Agricultural University, Copenhagen, Denmark
- Zhu J, Matsuzaki T, Lee F, Gonda Y (2003) Effect of gap size created by thinning on seedling emergency, survival and establishment in a coastal pine forest. *For Ecol Manag* 182:339–354
- Zirlewangen D, von Wilpert K (2001) Modelling water and ion fluxes in a highly structured, mixed-species stand. *For Ecol Manag* 143:27–37