

Spatial variability of summer microclimates and plant species response along transects within clearcuts in a beech forest

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Received 2 May 2005; accepted in revised form 8 December 2005

Key words: Air humidity, GAM, Light intensity, Spatial variation, Temperature gradient

Abstract

In a 4383 ha beech forest in central Belgium, we investigated whether, within clearcuts, microclimate gradients are detectable, and we tested for correlations between plant species composition and microclimatic heterogeneity. The results highlight a strong correlation between microclimatic parameters and distance from the forest edge. Of the 47 taxa found, 38 (81%) showed a significant change in expected occurrence in response to at least one of the investigated microclimatic parameters (air and soil temperature, air humidity, light intensity). The results suggest that a substantial number of forest herbaceous species with broad European distributions show particular microclimatic requirements. Furthermore, many species show a different response to combined factors, such as for instance soil temperature with increasing air humidity, which indicates that combinations of microclimatic parameters stronger determine the actual temperature, humidity or light levels at which species are expected to be present or not.

Introduction

It is well established that microclimate is critical to plant species for germination, growth and reproduction; and ecological processes, such as photosynthesis, evapotranspiration, nutrient cycling (e.g. Rosenberg et al. 1983; Woodward 1987; Jones 1992; Unwin 1997). Soil temperature and moisture are known to influence biotic and abiotic process rates, such as nutrient availability (Kimmins 1997), soil carbon sequestration/emission (Bowden et al. 1998), and microbial activity (Fisher and Binkley 2000). High temperature and moisture, together with active microbes and invertebrates, can also lead to a faster litter decomposition and thus facilitate establishment of

vegetation (Facelli and Pickett 1991). In a beech forest on limestone in Germany, Schmidt (2002) found that differences in the nitrogen content of the biomass along a gradient from forest to gap were influenced by radiation. In experimental conifer release treatments in Ontario, Reynolds et al. (2000) found that ammonium production was significantly correlated with soil temperature and moisture, increasing with temperature, and decreasing at higher moisture levels. Therefore, by examining the spatial variation of some microclimate parameters, one can estimate the spatial patterns of many biological processes.

Microclimate, especially the thermal regime of microenvironments, is often very important for forest management (Kimmins 1997). Many

authors have studied microclimate variability within different forest types (e.g. Chen and Franklin 1997; Xu et al. 1997), and numerous studies have focused on the effects of various management regimes on forest microclimate (e.g. Liechty et al. 1992; Brosofske et al. 1997; Zheng et al. 2000; Iverson and Hutchinson 2002). Although temporal and spatial microclimate fluctuations have been documented for many biotopes or through various ecotones, we know relatively little about microclimate sensitivity among species and across clearcuts.

Today, clearcutting in its various forms is the most widely used silvicultural system in the world (Matthews 1999). Of all forest management activities, it is clearcutting that has the greatest effect on temperature because of its alteration of the radiation-energy balance (Kimmins 1997). A better understanding of clearcut microclimates is therefore essential for both research on and management of forest resources. The contrasting microclimates between forest interior and clearcut is well documented (Chen et al. 1993; Barg and Edmonds 1999; Anderson and Leopold 2002; Schmidt 2002). Forest edge-interior microclimatic gradients were also frequently investigated (Chen et al. 1995; Renhorn et al. 1997; Williams-Linera et al. 1998; Gehlhausen et al. 2000; Newmark 2001; Cienciala et al. 2002), but, to our knowledge, very few studies focused on microclimate within clearcuts. Significant microenvironmental gradients may however occur within gaps, with the greatest exposures to high irradiances and temperatures skewed towards the north or south gap edges, especially at higher latitudes (Canham et al. 1990). In a former study, we found a spatial variability in the species presence and cover along transects into clearcuts (Godefroid et al. 2005). This could mean that microsites that are only a few meters apart may greatly differ in temperature or moisture regimes according to the distance to the forest edge.

This paper describes microclimate and plant species composition variation within clearcuts of an ancient beech forest in central Belgium. As climate plays a major role in the geographical distribution of plant communities, we hypothesise that microclimate, at the scale of a clearcut, may also affect the distribution of plant species. Specifically, we investigated gradients of air temperature and humidity, soil temperature and light

intensity within four locations. The objectives of this study are: (1) to investigate whether, within clearcuts, microclimatic gradients are detectable; and (2) to model the distribution of plant species along these gradients. Influences of edge orientation on plant species distribution were also studied. The ultimate goal was to improve our knowledge on microclimates and their possible influence on herbaceous vegetation within clearcuts, in order to help the interpretation and the prediction of biological phenomena associated with logging areas and to improve present forest management practices.

Materials and methods

Study area

The research was conducted in the Sonian Forest, south of Brussels (50°47' N; 4°26' E). This area has been proposed as a Site of Community Importance (Natura 2000 area, in fulfilment of the EC-Habitat Directive 92/43/EEC). It is a remnant of the forest that covered Western Europe after the last Ice Age. The forest covers an area of 4383 ha, 1654 ha of which are situated within the administrative limits of the Brussels Capital Region and constituting a management unit and being the area taken into consideration in the present study. Some 20,000 years ago, sandstone and flintstone formed the upper layer in the area of the Sonian Forest. After the last Ice Age, this layer was covered with loess. Today, almost the whole surface of the area (95%) is composed of a 3–4 m thick silt layer, which corresponds to the loess deposition. The forest ranges in altitude from 65 to 130 m a.s.l. The climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9 °C, annual precipitation is 835 mm. The natural vegetation is a deciduous forest in which oaks (*Quercus robur* and *Quercus petraea*) and beech (*Fagus sylvatica*) are the main species (Herbauts et al., 1996). Since the plantation work of the Austrian administration at the end of the 18th century, it is now composed of 74% of beech trees (*Fagus sylvatica*). Except beech, few other woody species are found. Sixteen percent of the forest surface is occupied by oak stands (*Quercus robur*) and 8% is represented by introduced conifer

stands (*Pinus sylvestris*, *Larix decidua*, *Picea abies*) (Vanwijnsberghe 2000).

Choice and demarcation of study sites

Orthophotos, soil maps and stand maps of the whole forest were examined in the G.I.S. Arc View (ESRI 1996), in order to detect the presence and age of clearcuts and to select the study sites. Four clearcuts were chosen in areas with comparable combinations of factors, i.e. forestry, pedological, geological, botanical aspects (Table 1). Clearcut borders were determined by examining orthophotos in Arc View. The crown of the last surrounding trees was used as criterion to demarcate the clearcuts.

Vegetation sampling

Within the four study sites, the herbaceous vegetation was sampled along a north–south and an east–west transect from one edge to the other, with points at 20 m intervals (sites A and B) or at 10 m intervals (sites C and D). Because clearcut B was characterised by an elongated shape in the NE–SW direction, the vegetation was sampled along two additional transects (NE–SW and NW–SE). We studied a total of 82 vegetation relevés (10 in site A, 30 in site B, 20 in site C and 22 in site D) on 18 transects on 4 m²-plots, which is the recommended area for grassland-like vegetation types (Kent and Coker 1992). The species composition was characterized by classical phytosociological plots (e.g. Westhoff and van der Maarel 1973), which means that total coverage for each species (vertical projection onto the ground) was estimated visually, and recorded within seven cover classes: *r*: 1 or 2 individuals; +: few indi-

viduals (<20) with cover <5%; 1: many individuals (20–100) with cover <5%; 2: 5–25% cover; 3: 25–50% cover; 4: 50–75% cover; 5: 75–100% cover. Since Braun-Blanquet cover-abundance values are not suitable for mathematical treatment, raw data were transformed by the corresponding cover percentage values (median of each scale interval): 0.2; 0.5; 2.5; 15; 37.5; 62.5 and 87.5 accounting, respectively for *r*; +; 1; 2; 3; 4 and 5 (arbitrary values were taken for *r*, + and 1).

Recording of microclimate variables

Measurements of microclimate variables were taken in each of the 82 sample plots. All variables were recorded during clear days within a timespan of 4 days around the summer solstice (23–26 June 2002) between 11:00 and 15:00 h, to get uniform and comparable radiation data (Geiger 1965; Hutchinson and Matt 1977; Aude and Lawesson 1998). Air temperature and moisture were measured 1 m above the ground with a pen-type thermohygrometer (range 0–50 °C; 2–98%). Soil temperature was measured at 7 cm below the ground level, with a strengthened metal probe of a IQ pH-volt-thermometer from Scientific Instruments, Inc. (West Palm Beach, FL, USA). Light intensity was measured using a Lutron LX-105 light-meter from Bioblock Scientific (Illkirch, France). The sensor was always placed horizontally at 1.8 m above the ground to avoid shadow from the operator (Aude and Lawesson 1998). Each measurement was represented by the average value of a continuous light record during 30 s. The position of each sample plot along the different transect directions was used to assess the influence of edge orientation on the species composition. Because the number of observations along NE–SW and NW–SE transects (only

Table 1. Physical and historical characteristics of four clearcuts (A, B, C, D) of the Sonian Forest.

Variable	A	B	C	D
Area (m ²)	9029	20852	5313	7897
Perimeter (m)	459	786	380	477
Ratio area/perimeter	19.67	26.53	13.98	16.56
Age (years)	13	5	5	13
Aspect	E	NE	NNW	NE
Elevation (m)	110–120	107–116	110–120	110–120
Mean slope (%)	6.3	3.9	9.0	8.1
Former stand	Fagus	Fagus, Quercus	Fagus	Fagus
Surrounding stands	Fagus	Fagus	Fagus, Quercus	Fagus

clearcut B) is very low when each aspect is studied separately, north-west and north-east-oriented samples are pooled into the north category, while south-west and south-east-oriented samples are pooled into the south category.

Data analyses

Effects of distance from the forest edge on clearcut microclimatic parameters were analysed by linear regression analyses (Spearman rank correlation coefficient r_s), using the package Statistica Version 6.0 (Statsoft 2001).

In order to check the orientation effect on the species, we used the Indicator Species Analysis for the different types of orientations (N, S, E, W), according to Dufrêne and Legendre (1997), as available in the PC-ORD package (McCune and Mefford 1997). The method combines information on the concentration of species abundance in a particular group of samples and the faithfulness of occurrence of a species in that group. It produces indicator values for each species in each group, which are tested for statistical differences using a Monte Carlo technique with 1000 permutations (Dufrêne and Legendre 1997).

The Canoco 4.5 statistical package (ter Braak and Šmilauer 2002) was used to summarise relationships between climatic variables and species using a regression model fitted with light intensity, air temperature, soil temperature and air humidity as predictors. A Generalised Additive Modelling regression (GAM; Hastie and Tibshirani 1990) was used with a cubic smooth spline function. GAM regression has been used in numerous studies of species–environment relationships (e.g. Bio et al. 1998; Austin 1999; Grytnes et al. 1999; Guisan and Zimmermann 2000; Heegaard 2002; Vetaas 2002) and was chosen because it does not assume any general shape of the response prior to the estimation (Austin and Meyers 1996). The model was tested with different degrees of smoothing. The optimum degree of smoothing (i.e. giving the best p -value for the deviance-based test) for each species was found to be 2. The response data are relative covers (subjectively estimate percentages) and therefore a Poisson distribution was assumed with a logistic link function.

Nomenclature follows Lambinon et al. (1998). The highly variable and taxonomically disputed

Rubus fruticosus agg. was considered a single species.

Results

Microclimate variations within the investigated clearcuts are shown in Figure 1. All relationships were highly significant. Air temperature increased with distance to the forest edge ($r_s=0.28$; $p=0.0121$). So did soil temperature and light intensity ($r_s=0.31$ and 0.51 , respectively; $p=0.0053$ and <0.0001 , respectively). Air humidity decreased with distance to the forest edge ($r_s=-0.37$; $p=0.0007$). Although all these microclimatic parameters show a similar gradient from the forest edge to the centre of the clearcut, the correlation among each other was weak ($0.10 < |r_s| < 0.43$; results not shown).

Correlations between clearcut shape (area, perimeter, ratio area/perimeter) or age and the magnitude of microclimatic gradients were not significant (results not shown), probably due to the low number of replicates ($n=4$). Edge exposure seems to have almost no effect as, according to the Indicator Species Analysis, only *Impatiens parviflora* and *Circaea lutetiana* were recognised as indicators for north and south edges, respectively ($IV=28.4$ and 12.0 ; $p=0.04$ and 0.02 , respectively).

Of the 47 taxa studied, 12 were significantly related to air temperature only (Appendix 1). Figure 2 presents the patterns of a few contrasting species. *Lonicera periclymenum* and *Impatiens parviflora* achieved a maximum response value at sites with 29 and 33 °C, respectively. *Luzula campestris* and *Polygonum hydropiper* preferred sites with higher summer temperatures, having an expected optimum exceeding 36 °C. *Scrophularia nodosa* had the reverse trend, preferring lower temperature, with a maximum response value at sites with 24 °C. Sixteen taxa were significantly related to soil temperature only (Appendix 1, Figure 3). Most of them showed a maximum response value at sites with 13 °C. *Myosotis arvensis* and *Luzula sylvatica* had the lowest optimum (11.5 °C), while *Rubus fruticosus* showed an increasing response with an expected optimum exceeding 14 °C. Thirteen of the taxa analysed had a statistically significant fit to air humidity only (Appendix 1, Figure 4). *Cardamine flexuosa* and *Dryopteris carthusiana* had an optimum at or

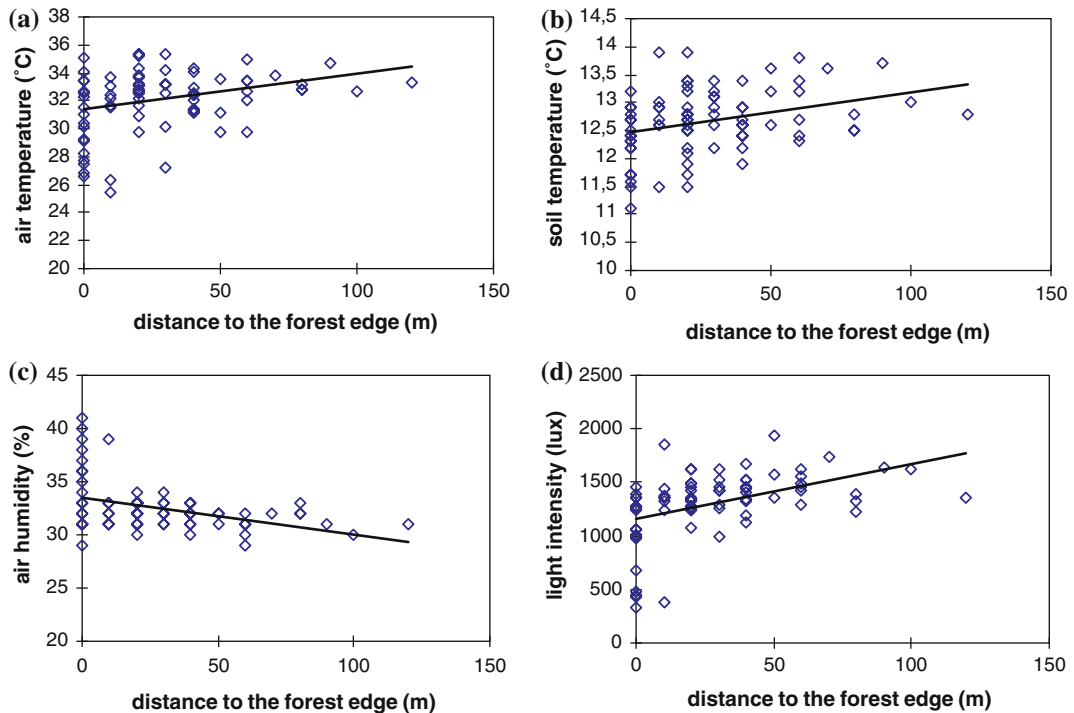


Figure 1. Microclimatic variations within the investigated clearcuts (Spearman's Rank Order correlations). (a) Air temperature; $r_s=0.28$; $p=0.0121$; $n=82$; $y=0.0255x+31.363$; (b) Soil temperature; $r_s=0.31$; $p=0.0053$; $n=82$; $y=0.0071x+12.469$; (c) Air humidity; $r_s=-0.37$; $p=0.0007$; $n=82$; $y=-0.0346x+33.496$; (d) Light intensity; $r_s=0.51$; $p<0.0001$; $n=82$; $y=5.1442x+1162.1$.

lower than 28% relative air humidity. *Anemone nemorosa* showed a narrow range with a maximum response value at 32%. *Luzula sylvatica* was the only species with an optimum higher than 42% humidity. Seven taxa were significantly related to light intensity only (Appendix 1, Figure 5). The narrowest range was observed for *Lapsana communis* showing a maximum response value at 1500 lux, while, surprisingly, *Anemone nemorosa* showed an optimum higher than 2000 lux.

Further, some microclimatic parameters which were not statistically significant for particular species when taken alone, became significant when treated as an additional effect (Figure 6; Appendix 1). For instance, soil and air temperature taken separately did not significantly explain the distribution of *Agrostis stolonifera* or *Holcus lanatus*, whereas their combination gave a significant result. So did the combination of air humidity and air temperature which significantly influenced the distribution pattern of *Athyrium filix-femina*, while they did not when taken separately. Seven taxa, for which there were no apparent relationship with any of these microclimatic parameters taken separately,

became significantly related to combinations of these parameters (Appendix 1). For instance, it appeared that *Centaurium erythraea* and *Dactylis glomerata* had an optimum at high air temperature and low air humidity, but the latter needed high light intensity and low soil temperature in contrast to the former. Taxa such as *Lapsana communis* and *Luzula pilosa* never occurred in sites above 35 and 33% air humidity, respectively. Of the species preferring well-lit places, *Deschampsia flexuosa*, *Galium aparine*, *Holcus lanatus*, *Juncus effusus* and *Stachys sylvatica* were not expected to appear in sites with light levels below 1000 lux. Other microclimatic requirements characterised *Epilobium angustifolium* and *Dryopteris dilatata* which need high air humidity and soil temperature.

Discussion

Clearcuts show microclimate spatial variability

The results demonstrate that microclimatic parameters, such as air temperature, soil temper-

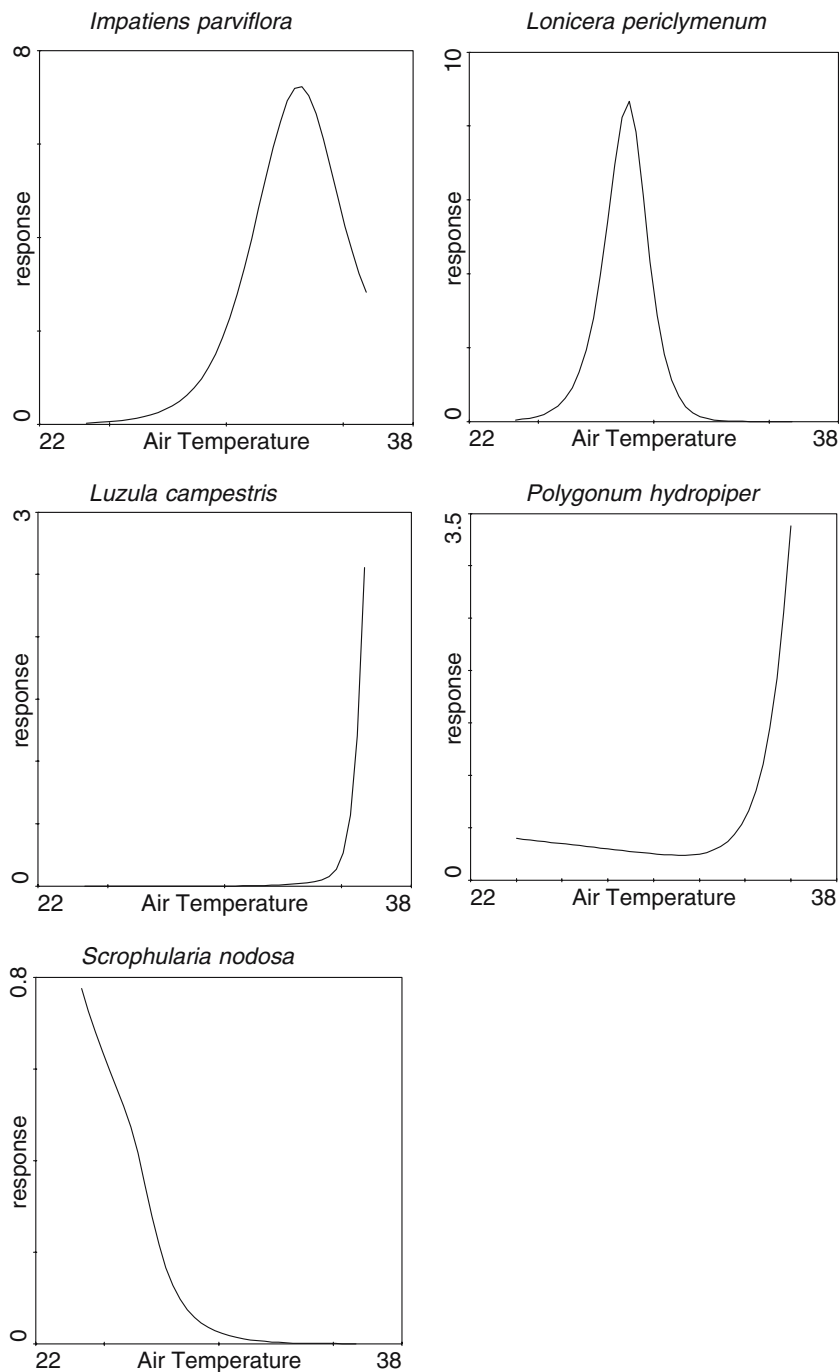


Figure 2. The response (estimated percentage cover values) of species significantly related to air temperature ($^{\circ}\text{C}$), according to the GAM procedure. Only the patterns of a few contrasting species are presented. Regression results for all species are shown in Appendix 1.

ature, air humidity and light intensity, show a high spatial variability within clearcuts. This variability was strongly influenced by the distance from the forest edge. With an amplitude of 10°C along a

120 m-gradient (maximum we could observe), air temperature was spatially more variable than soil temperature, the latter showing an overall difference of only 2.8°C along the gradients.

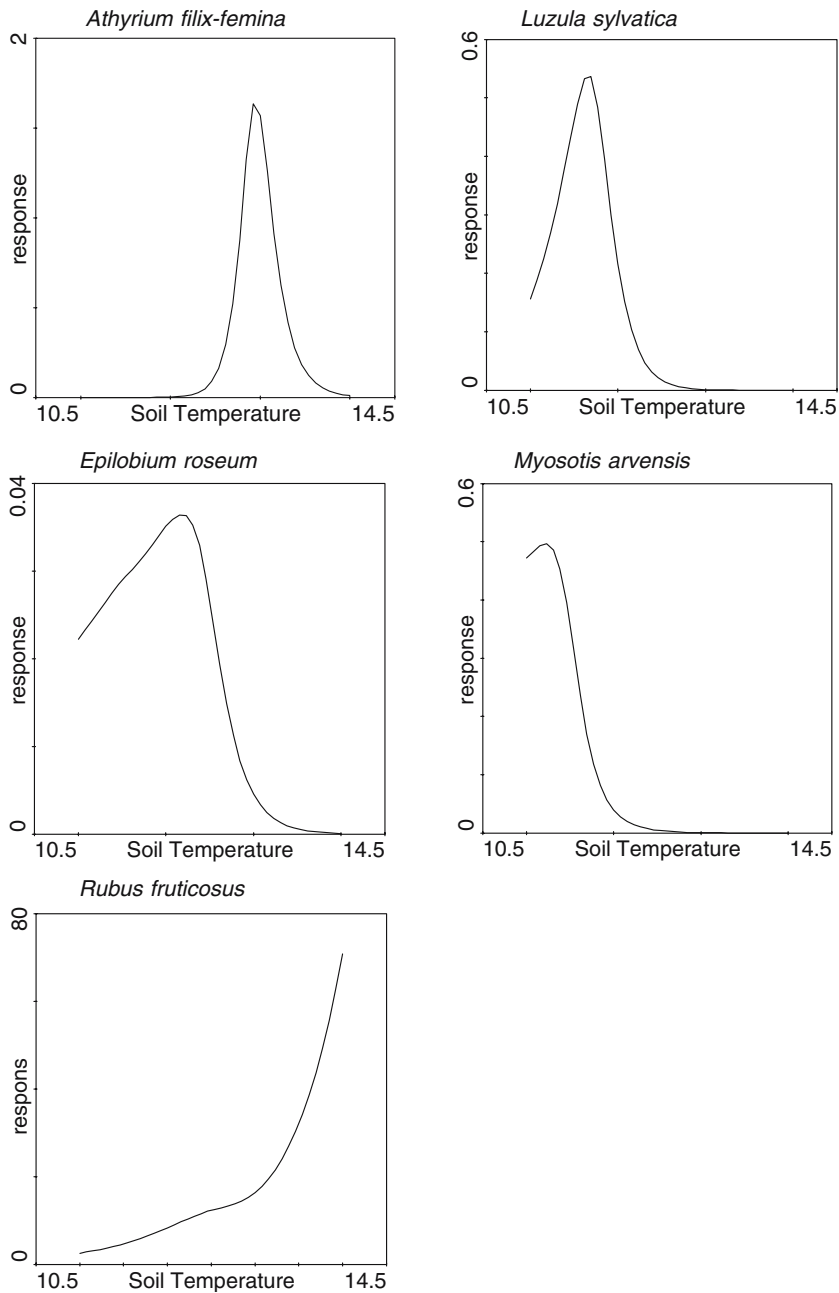


Figure 3. The response (estimated percentage cover values) of species significantly related to soil temperature ($^{\circ}\text{C}$), according to the GAM procedure. Only the patterns of a few contrasting species are presented. Regression results for all species are shown in Appendix 1.

As topography was similar throughout our study sites, it means that this physical parameter cannot account for the observed gradients, and it suggests that the influence of the surrounding forest – through the so-called “edge-effect” – is the most probable explanation. However, there is

a substantial discrepancy among recent studies on the existence and intensity of edge effects (Murcia 1995), and the question would be here: what kind of phenomenon initiated this edge-effect expressed through microclimate gradients, and what is the depth-of-edge influence, or edge width? The depth

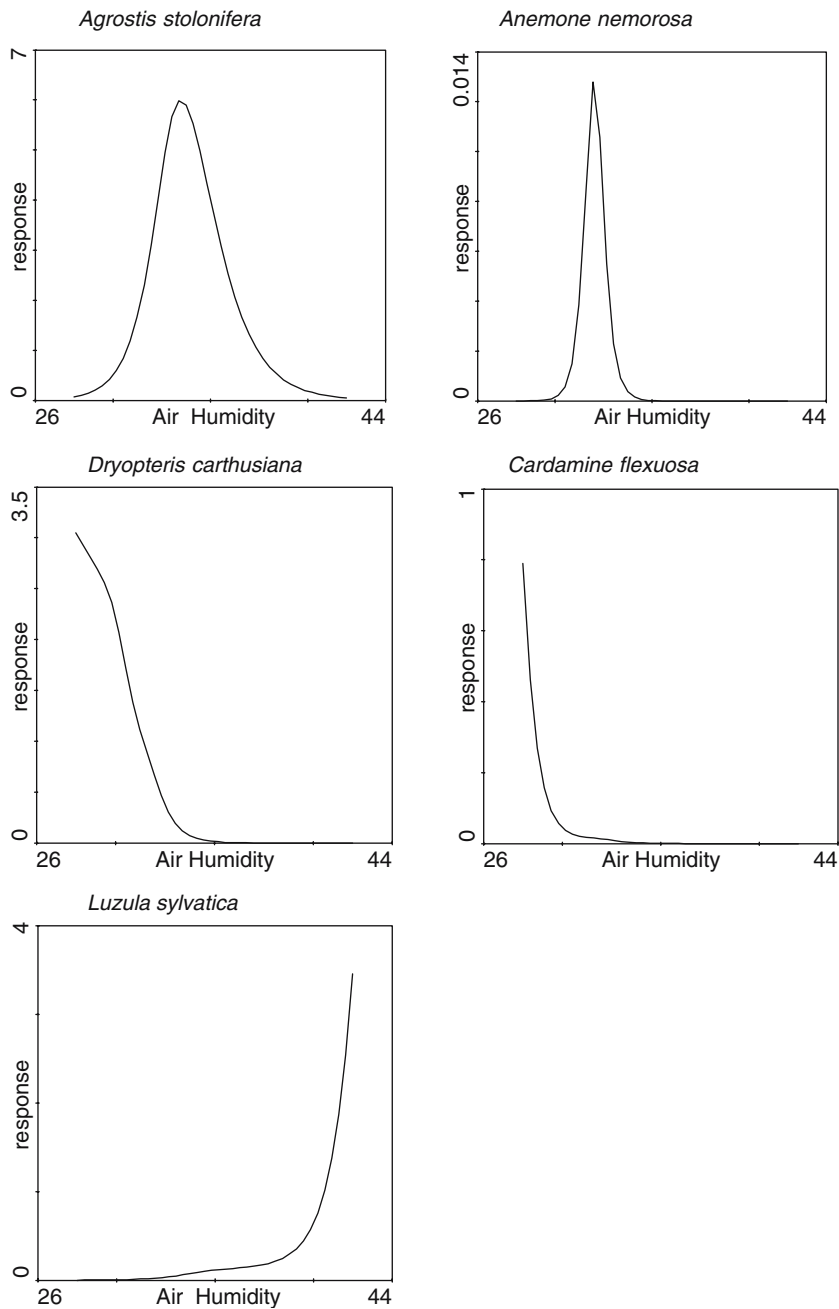


Figure 4. The response (estimated percentage cover values) of species significantly related to relative air humidity (%), according to the GAM procedure. Only the patterns of a few contrasting species are presented. Regression results for all species are shown in Appendix 1.

to which light penetrates within the clearcut is dependent on forest stands in the vicinity, and the distance to which shade extends from a stand edge into the adjacent opening was a priori assumed to play an important role. Nevertheless, the observed microclimatic gradients are striking as we sampled

near to the summer solstice and around midday, i.e. when the sun has the highest angle, so the clearcut is fully sunlit at this time. For instance, in the study area (51° N), at noon (clock time) and at solstice, solar angle is 62°, thus the 35 m tall edge trees cast a 16 m long shadow. As microclimatic

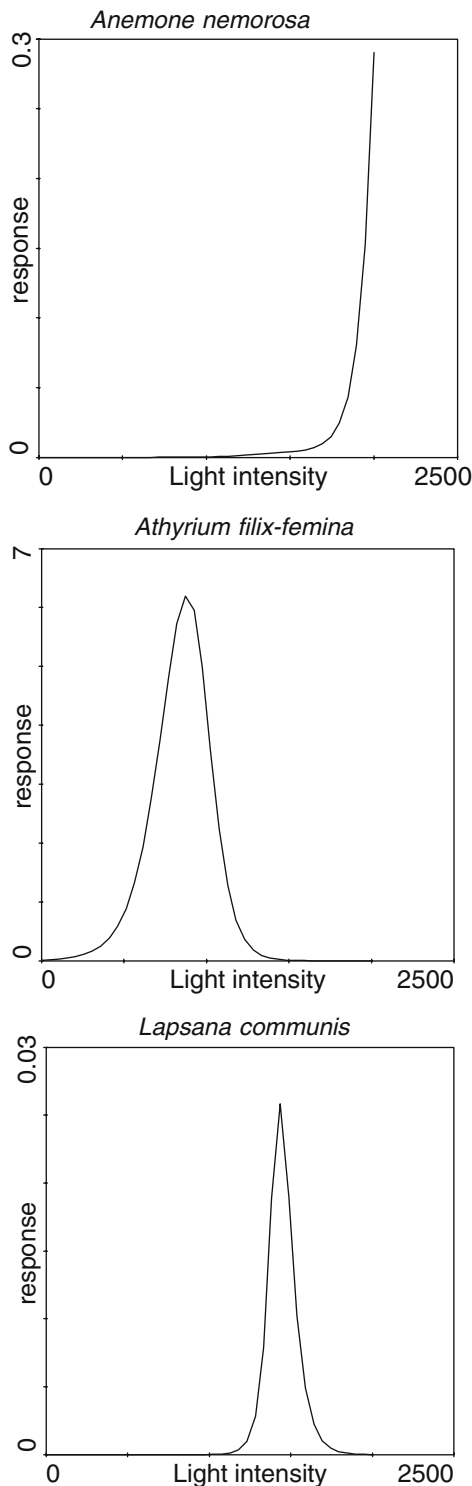


Figure 5. The response (estimated percentage cover values) of species significantly related to light intensity (lux), according to the GAM procedure. Only the patterns of a few contrasting species are presented. Regression results for all species are shown in Appendix 1.

gradients obtained from our data extend far beyond this distance, it suggests that the shade provided by the adjacent forest is not the only factor explaining the spatial variability obtained in our system. Chen et al. (1993) have shown that daily averages of air and soil temperature are consistently lower, and air humidity is higher, inside the forest than in the clearcut or at the edge. Therefore, the patterns observed in the clearcut microclimates are probably closely related to the diffuse influence of the colder and wetter forest mass in the vicinity. So, it is likely that warming at the forest edge triggers convection which transports cooled air from the forest to the clearcut. This particular microclimate surrounding the patches might be responsible for the gradually decreasing air humidity and increasing air temperature within the clearcuts, and would account for the narrow range observed in the soil temperature differences, as the forest atmosphere is expected to have a stronger influence on the aboveground microclimatic parameters than on soil microclimate. Gradients in microclimate from one patch into neighbouring patches were already highlighted by Murcia (1995) and Chen et al. (1999), but from a clearcut into a forest stand, i.e. the opposite of what we did in the present study. Results of Gehlhausen et al. (2000) and Newmark (2001) indicate that microclimatic variables differ in the degree to and the distance over which they show an edge effect. In their study on the edge effect of forest fragments, Gehlhausen et al. (2000) found that relative humidity showed the widest gradient, while light and soil moisture had the steepest gradients. In our system, microclimatic gradients were perceptible as far as the midpoint of the clearcuts, i.e. up to 120 m from the edge. Because the maximum patch length was 240 m, we could not test how microclimate develops over longer distances, but it becomes definitely clear that the percentage of area-of-edge influence in our study sites is much higher than the percentage of harvested area alone. According to Chen et al. (1999), the depth-of-edge influence, although it varies over times and with edge characteristics, can extend four to six tree heights into the forest from a recent clearcut edge. If we transpose this into our system, it is equivalent to an edge-effect of approximately 200 m into the clearcuts from the forest edge. For some variables, such as air movement, edge width might even extend up to 15

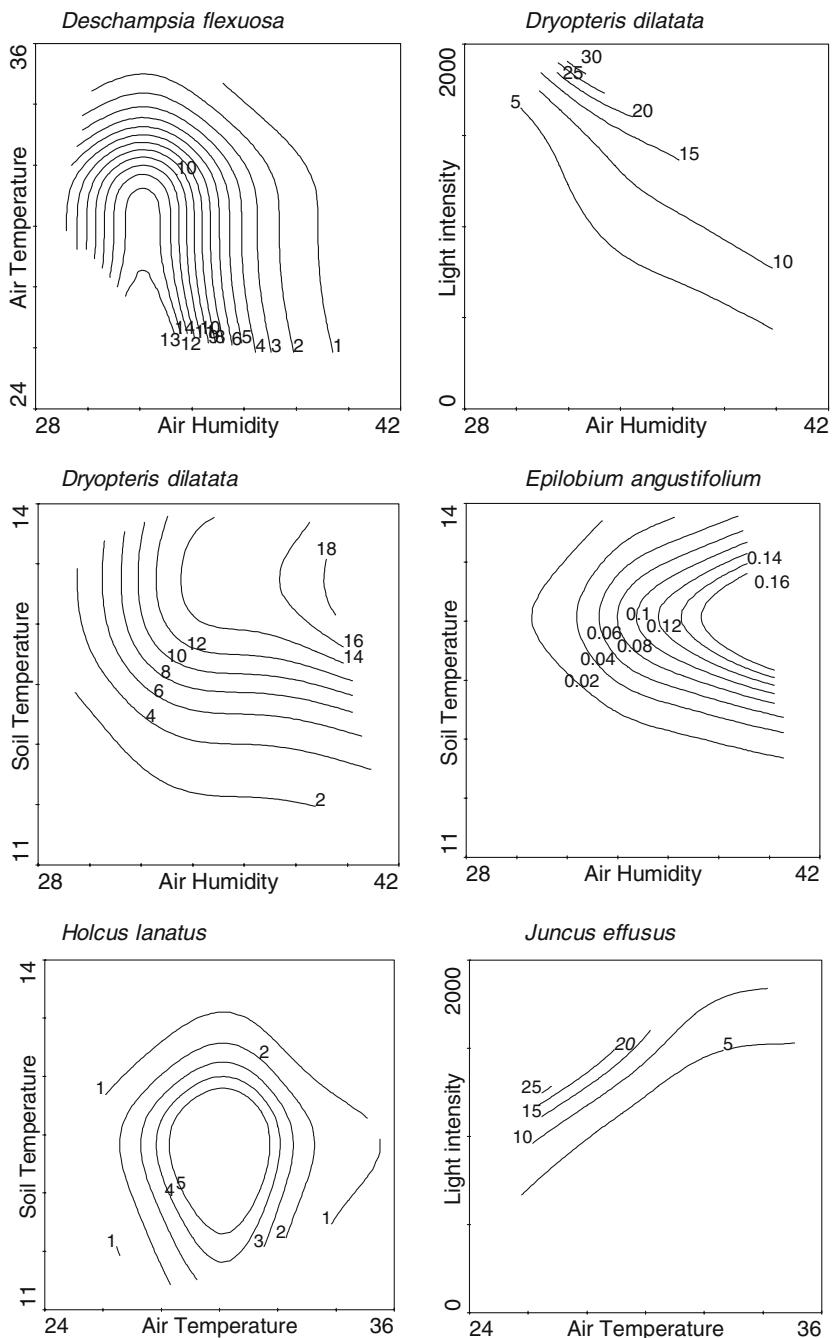


Figure 6. Contour plots of the response of species with distributions that are significantly related to combinations of microclimatic parameters which alone were not significant. Only the patterns of a few contrasting species are presented. Regression results for all species are shown in Appendix 1.

tree heights into the clearcut (Rosenberg et al. 1983). When this number is translated to our area, it would correspond to a edge effect of about 500 m.

The variance among values measured at each distance along the transects was high but, interestingly, it decreased with the distance from the edge, suggesting that clearcut edges have more

heterogeneous microclimates compared with clearcut interior, which is consistent with the statement of Gosz (1991) concerning ecotones. Chen et al. (1993), who studied temporal variations of climatic parameters in an old-growth *Tsuga heterophylla* forest, have shown that winds are stronger in clearcuts, which helps mix air and reduces variation in air temperature and relative humidity. This may be the cause for the highest variability in microclimate at the edge, rather than in clearcut interior, but the primary reason would be the influence related to edge orientation (Chen et al. 1993). According to former studies, edge orientation plays a critical role for all microclimate variables; for air and soil temperature and humidity, it affects the times of the day at which maximum and minimum values peaked (Chen et al. 1993, 1995). Gehlhausen et al. (2000) also highlighted the existence of more pronounced edge effects on south and west edges. Nevertheless, in our study, edge orientation did not significantly affect any of the microclimate variables under consideration, which explains that almost no species (only two of them) showed a response to the edge orientation. This is probably because plants integrate daily or seasonally microclimate variations and extremes, while we deal with unique measurements taken at noon and at summer solstice, which considerably reduces a possible edge orientation-effect.

Species distribution as related to microclimates

Of the 47 taxa analysed, 38 (81%) showed a significant change in expected occurrence in response to at least one of the investigated microclimatic parameters, indicating that clearcuts show environmental transitions of importance for species distribution. Furthermore, our results suggest that many species change their response to, say, soil temperature with increasing air humidity, or to light intensity with increasing air temperature. This indicates that combinations of microclimatic parameters stronger determine the actual temperature, humidity or light levels at which species are expected to be present or not.

The present paper gives an insight of plant species behaviour related to microclimate, which can corroborate, but also usefully complement, existing information on species ecology. Certain unex-

pected, but not less interesting, patterns have shown some unknown species responses, particularly for forest species. For instance, *Rubus fruticosus* agg., which is known for its response to light availability (Wehrlen 1985), showed in our study area a strong response to soil temperature and not to light intensity. The unsuspected avoidance of some species of particular habitat conditions is probably due to increased stress caused by temperature-, humidity- or light-related physiological processes. These findings provide interesting information on microclimatic requirements of some herbaceous species with a large European distribution. It also highlights that species belonging to the same ecological group (and having thus theoretically the same ecological requirements), can actually show totally different responses to microclimate parameters. This underlines the need for defining ecological species groups (i.e. assemblages of co-occurring plant species exhibiting similar environmental affinities) not only based on edaphical requirements but also on microclimatic affinities. While effects of climate, and especially climate change, on plant species are rather well documented (e.g. Fox et al. 1999; Duckworth et al. 2000; Walther 2000), very few studies have focused on the possible influence of small microclimatic gradients on plant species distribution, which is definitely an underexploited research field. Indeed, except the pioneering work of Ellenberg (1974) giving, for almost all plant species of Central Europe, a light and temperature index indicating the conditions under which each species is usually found, we do not know other works aiming at quantifying species optima for microclimate parameters.

Methodological considerations

The microclimatic environment and its relative importance for driving biological processes vary with temporal and spatial scales, because ecosystem structure and function are scale dependent (Meentemeyer and Box 1987). Thus, relationships between microclimate and structural landscape features or ecosystem processes developed at any scale of study may not be applicable at other scales (Levin 1992). Therefore, our preliminary results need to be completed with additional data for different site conditions in order to evaluate

whether generalisations can be made regarding clearcut microclimates. Also, Chen et al. (1995) and Newmark (2001) emphasised that forest edge microclimatic gradients are temporally non-constant. So, because microclimatic variables respond differently depending on time of day, it would be desirable to collect new data over the course of the day over one or two growing seasons, as Chen et al. (1995) and Xu et al. (2002) did. For examining microclimate variables in clearcuts, it would be interesting to follow the example of Fleming et al. (1998) and use daily maximums and daily minimums. On the other hand, when studying microclimates in clearcut, edge and interior forest, Chen et al. (1993) found that the microclimates at the edge and the clearcut show a variable relationship with regard to averages and differences. Therefore, using daily averages as well as daily differences (i.e. maximums minus minimums) is highly desirable. Seasonal extremes, the number of frost days and sunless days, as well as spectral light differences (e.g. ratio far red/red) might also certainly gather more results. Another possible refinement of the method would be to consider more variables, following the example of Chen et al. (1995), in their study on microclimatic gradients in stands of old growth Douglas forest in the Pacific Northwest. Besides air temperature, soil temperature and relative humidity, they also

collected data for soil moisture, short-wave radiation and wind speed. Soil moisture is indeed expected to play an important role as already pointed out by Anderson and Leopold (2002) who found that the individual factors influencing species richness at the gap scale were depth to water, water level fluctuation and microtopographic variability, indicating the importance of hydrology over light as a species control. Further studies focusing on plant species response in relation to microclimate should take all these aspects into consideration, in order to improve our knowledge of species ecological behaviour.

Acknowledgments

Most analyses synthesised in this paper were performed with financial support provided by the Brussels Institute for Environmental Management (B.I.M.).

Appendix 1

Regression results for species on air humidity, air temperature, soil temperature and light intensity.

	Predictor	Null dev.	Fitted dev.	Res.df	F	p
<i>Agrostis stolonifera</i>	AirH	1251.40	1043.42	79.1	3.22	0.047531
	AirT + SoilT	1251.40	967.26	77.1	2.92	0.027385
<i>Anemone nemorosa</i>	AirH	2.97	2.22	79.0	6.00	0.003738
	Light	2.97	1.88	79.1	3.32	0.042971
<i>Athyrium filix-femina</i>	Light	328.84	164.42	79.1	20.13	< 1.0e-6
	SoilT	328.84	240.23	79.1	4.25	0.018885
	AirH + AirT	328.84	201.24	77.1	5.06	0.001269
<i>Cardamine flexuosa</i>	AirH	8.72	6.68	79.1	3.46	0.037699
<i>Centaurium erythraea</i>	AirH + AirT	9.28	7.27	77.1	2.57	0.046221
	AirH + Light	9.28	6.80	77.1	3.39	0.013534
	AirT + Light	9.28	6.76	77.1	3.68	0.009076
	AirT + SoilT	9.28	7.33	77.2	2.62	0.043680
<i>Dactylis glomerata</i>	AirH + Light	158.47	121.63	77.1	2.62	0.042365
	AirH + SoilT	158.47	114.86	77.1	3.29	0.016315
	AirT + SoilT	158.47	110.72	77.2	3.83	0.007589
	Light + SoilT	158.47	112.76	77.1	3.95	0.006240
<i>Deschampsia flexuosa</i>	AirH + AirT	2150.33	1787.85	77.1	2.58	0.045665
	AirT + Light	2150.33	1666.56	77.1	3.53	0.011257
<i>Digitalis purpurea</i>	AirT	10.46	6.59	79.0	14.83	0.000003
<i>Dryopteris carthusiana</i>	AirH	297.43	244.37	79.0	3.50	0.035475
<i>Dryopteris dilatata</i>	AirH + Light	1606.97	1346.52	77.0	2.68	0.038174
	AirH + SoilT	1606.97	1367.69	77.1	2.63	0.041164
	Light + SoilT	1606.97	1342.51	77.0	2.91	0.026658

Appendix 1. (Continued)

	Predictor	Null dev.	Fitted dev.	Res.df	F	p
<i>Epilobium angustifolium</i>	AirH + SoilT	10.25	8.22	77.1	2.51	0.049798
<i>Epilobium roseum</i>	SoilT	8.72	7.17	79.1	3.50	0.036886
<i>Epilobium tetragonum</i>	SoilT	6.14	5.01	79.1	3.26	0.045316
<i>Galium aparine</i>	AirT	131.49	96.95	79.0	4.13	0.019628
	SoilT	131.49	94.70	79.1	4.69	0.013164
	AirH + Light	131.49	86.58	77.0	2.82	0.030734
<i>Galeopsis tetrahit</i>	AirT + SoilT	25.48	18.00	77.1	3.72	0.008738
<i>Hieracium umbellatum</i>	Light	1122.83	911.20	79.1	3.84	0.027205
<i>Holcus lanatus</i>	AirH	1061.75	869.80	79.0	4.09	0.020134
	AirT + Light	1061.75	753.61	77.0	3.08	0.021214
	AirT + SoilT	1061.75	809.05	77.2	2.90	0.029155
	Light + SoilT	1061.75	778.80	77.2	3.94	0.006536
<i>Impatiens parviflora</i>	AirT	1666.01	1481.29	79.1	3.17	0.049730
<i>Juncus effusus</i>	AirT + Light	1270.27	1012.78	77.0	3.16	0.018546
<i>Lapsana communis</i>	Light	5.33	3.89	79.0	5.61	0.005257
	AirT + AirH	5.33	3.72	77.2	2.88	0.029662
	AirH + SoilT	5.33	3.53	77.0	4.58	0.002259
<i>Lonicera periclymenum</i>	AirH	551.67	388.81	78.0	3.28	0.025357
	AirT	551.67	261.78	79.1	28.30	< 1.0e-6
	SoilT	551.67	367.95	79.0	6.84	0.001824
<i>Lotus corniculatus</i>	AirH	7.43	5.14	79.1	7.18	0.001591
	AirT	7.43	4.13	78.1	12.54	0.000001
<i>Luzula campestris</i>	AirH	25.27	19.09	79.1	4.15	0.020897
	AirT	25.27	14.96	79.0	11.40	0.000048
	SoilT	25.27	17.65	79.0	6.32	0.002840
<i>Luzula multiflora</i>	AirT	226.45	176.89	79.1	4.21	0.020027
<i>Luzula pilosa</i>	AirT	24.00	17.48	79.1	5.60	0.005753
	SoilT	24.00	17.52	79.1	4.98	0.009946
	AirH + Light	24.00	13.93	77.0	8.35	0.000012
<i>Luzula sylvatica</i>	AirH	38.19	22.65	79.0	7.45	0.001137
	SoilT	38.19	18.81	79.1	24.37	< 1.0e-6
<i>Moehringia trinervia</i>	AirH	2.97	1.89	79.1	9.13	0.000324
	SoilT	2.97	2.37	79.1	3.31	0.043676
<i>Myosotis arvensis</i>	AirH	22.37	16.46	79.1	4.08	0.022337
	AirT	22.37	11.31	79.1	23.55	< 1.0e-6
	Light	22.37	15.94	79.1	4.62	0.014068
	SoilT	22.37	11.37	79.0	16.25	0.000001
<i>Polygonum hydropiper</i>	AirT	175.09	145.79	79.0	4.54	0.013377
<i>Pteridium aquilinum</i>	AirH + Light	1836.87	1362.88	77.1	3.20	0.018589
<i>Ranunculus repens</i>	Light	6.14	3.93	79.1	9.76	0.000192
	SoilT	6.14	4.82	79.1	4.20	0.019732
<i>Rubus fruticosus</i> agg.	SoilT	3438.85	2884.00	79.0	5.53	0.005794
<i>Rumex acetosella</i>	Light	1.76	1.31	79.0	4.15	0.019262
	SoilT	1.76	1.24	79.0	5.29	0.006950
	AirT + AirH	1.76	1.11	77.0	4.64	0.002080
<i>Scrophularia nodosa</i>	AirH	22.68	13.74	79.0	10.47	0.000107
	AirT	22.68	11.71	79.0	20.60	< 1.0e-6
	Light	22.68	16.16	79.1	5.06	0.009590
	SoilT	22.68	15.90	79.1	6.55	0.002699
<i>Stachys sylvestris</i>	AirH + Light	236.50	183.15	77.2	2.78	0.034494
<i>Stellaria media</i>	SoilT	25.83	19.87	79.1	4.27	0.018547
	AirT + Light	25.83	19.03	77.2	2.85	0.031579
<i>Teucrium scorodonia</i>	AirT	291.70	200.47	79.0	12.10	0.000030
<i>Urtica dioica</i>	AirH	16.94	14.88	79.0	3.52	0.035303

AirH = air humidity; AirT = air temperature; SoilT = soil temperature; Light = light intensity. Null dev. = null model deviance; Fitted dev. = fitted model deviance; res. df = fitted model residual degree of freedom; p = p -value for F -test. Only significant relationships ($p < 0.05$) are reported.

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