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Growth of *Fagus sylvatica* saplings in an old-growth forest as affected by soil and light conditions

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Introduction

The biological reserve of La Tillaie (Fontainebleau forest, 50 km south of Paris) has been studied by many scientists working on vegetation (Pontailler 1979; Faille 1980; Faille et al. 1984; Koop & Hilgen 1987; Lemée 1990; Peltier et al. 1997) and soil (Robin 1970; Robin & Deconinck 1975; Lemée 1975; Faille 1975a, b; Fardjah et al. 1980; Ponge & Delhay 1995). The favourable influence of gaps in the canopy on the development of common beech (*Fagus sylvatica*) seedlings and saplings was established by Pontailler (1979) and his results were used to understand renewal of the beech ecosystem, confirming observations by Watt (1923) on British beech woods. Nevertheless work recently done on this site indicated that seedlings (2-yr-old) and reacted in a quite different way than young saplings (5-yr-old) to light conditions (Peltier et al. 1997). Other observations on the same site and data in the literature (Harley 1949; Weissen et al. 1986; Delhay & Ponge 1993; Ljungström & Stjernquist 1995; Ponge & Delhay 1995) indicated detrimental influence of dysmoder humus and soil acidity on the growth and survival of beech seedlings.

Differences in sapling development according to site conditions may have a bearing on regeneration problems which selectively affect beech stands according to light and soil conditions (Weissen et al. 1986). In particular, better development of the root system in some sites than in others may increase the ability of the young tree individual to withstand drought periods (Weissen & Jacqmain 1978) or damages to aerial parts caused by herbivory.

The purpose of our study is to reexamine the influence of both humus and light conditions on the growth and development of beech saplings by sampling individuals directly in the field. This approach provides an opportunity to take into account all possible combinations of environmental factors.

Study site

1 The biological reserve of La Tillaie is located within the Fontainebleau forest (50 km south of Paris,
2 France). Beech is dominant, having replaced oak during the last four centuries without any
3 management (Lemée 1990). Old oak (*Quercus petraea*) individuals are present only in places where
4 beech was disfavoured by the absence of limestone in the subsoil. This old-growth forest is
5 characterized by a great variety of soil and light conditions due to strong heterogeneity of the parent
6 rock and mosaic patterns associated with gap dynamics (Watt 1947). On most of the plain surface the
7 parent rock is fine Fontainebleau sand with a low clay content (<5%), overlying limestone, the clay
8 content increasing abruptly in depth at the contact with limestone. Except in the zone where oak is still
9 present, beech trees are tall: mature ones average 40 m in height and 95 cm in diameter at breast
10 height. Humus may vary from oligomull to hemimoder (Brêthes et al. 1995; Jabiol et al. 1995) in the
11 zones where sand is underlain by limestone, and from eumoder to dysmoder in zones where sand is
12 underlain by sandstone, the latter have relictual individuals of oak (Ponge & Delhay 1995). Other
13 information on plant communities and nutrient cycles is given by Lemée (1978).

14

15 During the two previous years a strong defoliation by gypsy moth (*Lymantria dispar*) caterpillars
16 occurred on beech (seedlings and saplings included) over the whole Fontainebleau forest.

17

18

19 **Material and methods**

20

21 We collected 41 five-yr-old beech individuals distributed over the whole study area (33ha), in as varying
22 light and soil conditions as possible. All saplings visible in a wandering tour were sampled. A sapling
23 age of 5 years was chosen because 1989 was the most recent mast year. Sampling was done within a
24 2-week period in August 1994.

25

26 Saplings were excavated, separated into aerial and subterranean parts, rapidly transported to
27 the laboratory in plastic bags, then described the same day. After all measurements were made (Table
28 1), plant parts were oven-dried for 2 days at 40°C, then weighed. Environmental conditions were
29 recorded in the field for each sapling using simple methods, except for pH H₂O which was measured in
30 the laboratory in a 1:2 soil:water (w/w) suspension (Table 2). Litter was described by thickness of OL
31 (entire leaves), OF (fragmented leaves) and OH (fine organic matter) horizons, measured after

1 trenching the topsoil with a sharp knife just near the place where saplings had been excavated.
2 Munsell® Soil Color Charts (Macbeth Division of Kollmorgen Instruments Corporation, Baltimore,
3 Maryland) were used to describe the underlying A horizon at three different depths (3, 6, and 9 cm).
4 The use of these charts allows to quantify three distinct features. The colour index, varying from 7.5 YR
5 to 10 YR in the studied sample, indicates the passage from red to yellow in the yellow-red range, the
6 red colour being mainly due to iron staining. The value index, varying from 3 to 6 in the studied sample,
7 increases when the A horizon becomes lighter, which is mainly due to a decrease in the content of
8 dark humified organic matter. The chroma index, varying from 0 to 8, increases when the colour
9 becomes brighter. Thus the colour of the A horizon can be quantified by three independent
10 measurements. Variations of these morphological features according to depth were assessed by
11 measuring Munsell® parameters at three different depths. This method was thought to give more
12 reliable information about humus condition than humus form, which varies from mull to moder in the
13 studied sample. Nevertheless, when necessary, reference will be made in the discussion to humus
14 forms as defined by Brêthes et al. (1995). Mull is characterized by an A horizon (organo-mineral
15 horizon located just under the litter layer) made of earthworm faeces (macro-aggregates) where
16 organic matter is thoroughly mixed with mineral matter (clay-humus complexes). Mull humus forms
17 may vary in number and thickness of litter horizons: eumull is characterized by the absence of an OF
18 horizon (OL only), oligomull by the presence of a thin OF horizon (OL+OF), dysmull by the presence of
19 a thick OF horizon (OL+OF), and amphimull by the presence of an OH horizon (OL+OF+OH). Moder is
20 characterized by an A horizon made of mineral matter (generally sand or silt particles) juxtaposed to
21 organic matter (small holorganic animal faeces), without visible mixing by earthworms. Like in mull
22 humus forms, litter horizons may vary in thickness, amphimull being characterized by the absence of
23 an OH horizon (OL+OF), eumoder by the presence of a thin OH horizon (OL+OF+OH), and dysmoder
24 by a thick OH horizon (OL+OF+OH).

25

26 Data were analysed by correspondence analysis, a multivariate method using the chi-square
27 distance (Greenacre 1984) to order data points (here saplings, morphological and environmental
28 parameters) in a multi-dimensional mathematical space. After calculation of eigenvalues of the chi-
29 square distance matrix, the cloud of data points was projected in the space determined by the higher
30 eigenvalues (first factorial axes). Correspondence analysis allows simultaneous projection of rows and
31 columns of the data matrix in the space defined by the factorial axes. Morphological parameters (Table

1 1) were used as active variables (contributing to factorial axes) and environmental parameters (Table
2 2) as passive ones (projected as if they had participated but without any influence on the factorial
3 axes). Variables (active and passive) were transformed previous to analysis by reweighting and
4 focusing (mean = 10; standard deviation = 1), thus smoothing out the effect of varying measurement
5 scales (cf. Ponge & Delhayé 1995). To each active variable was associated a conjugate variable of
6 similar mean and standard deviation but varying in opposite sense (complementation to 20). This has
7 proven useful when a possible size effect is suspected, like in this sample (Arpin et al. 1984). Thus 34
8 $\times 2 = 68$ active variables were used in the analysis.

9

10 To test for possible effects of environmental factors displayed by correspondence analysis and
11 others, one-way analyses of variance (ANOVA) were applied to morphological data sets (cf. Sokal &
12 Rohlf 1995).

13

14

15 **Results**

16

17 All morphological variables and environmental parameters, together with individual saplings, were
18 projected as points in the plane of the first two axes of correspondence analysis, which extracted 26%
19 and 8% of the total variance, respectively (Fig. 1). The most striking differences between saplings
20 could be attributed to their size, this effect being reflected by axis 1. On the negative side of this axis
21 were placed large saplings (1+, 21+, 7+ to 11+, 4+ to 6+), with a high number of leaves (17+), and
22 deep rooting (22+). These saplings were opposed to small ones, with opposite features. Some
23 environmental variables (passive variables) obtained high loadings and long vector projections along
24 axis 1, e.g. Munsell® value at 6 cm (H) and 9 cm (I) and thickness of the OF horizon (B). Thus large
25 saplings (placed to the left on the diagram) were found in places with dark A horizons (H- and I-) and
26 much litter in the OF horizon (B+) which, in the particular conditions of this site, were characterized by
27 a hemimoder or moder humus form, compared to oligomull where the A horizon was light-coloured and
28 the OF horizon thin.

29

30 Given the results of correspondence analysis, two groups of saplings formed on the basis of
31 Munsell® value at 6 cm depth were compared by analysis of variance (Table 3). Morphological

1 features associated with axis 1 of correspondence analysis were well-reflected in this analysis, except
2 for stem diameters of the first (7) and fifth (11) years, and annual growth increments of the third (4) and
3 fourth (5) years which did not prove significantly different between these two groups.

4
5 Other important variation in sapling morphology was reflected in axis 2 of correspondence
6 analysis (Fig. 1). Saplings on the positive (upper) side of axis 2 were poorly ramified (20-), with a low
7 shoot/root ratio (34-), thin leaves (18-), but deeply rooted (22+, 24+ to 30+), with a high rate of
8 mycorrhization (31+, 32+), and little deformation of root apices (33-). These features indicated a strong
9 development of subterranean parts compared to aerial parts. Opposite features were shared by
10 saplings placed on the negative (lower) side of axis 2. Thus the former group seemed more firmly
11 established (better development of the root system) than the latter one, independently of sapling size.

12
13 Environmental variables with high positive loadings on axis 2 were incident light during morning
14 hours, i.e. from sunset to 10.30 AM (R, S), ground vegetation (W), thickness of the OL horizon (A), and
15 darkness of the A horizon at 9 cm depth (F). These features did not seem directly associated with the
16 degree of opening (U, V). The relationships between incident light coming from south-east (7.30 to
17 10.30 AM) and morphology of saplings were tested by help of analysis of variance (Table 4). This
18 showed a significant decrease in the rooting depth and length of deep lateral roots, the rate of
19 mycorrhization by *Cenococcum geophilum*, and an increase in the deformation of root apices when
20 some incident light comes from south-east (irrespective of other hours of light), but no significant
21 differences in aerial parts or shoot/root ratio.

22
23 The possible influence on sapling size of canopy aperture and total light, factors not evidenced
24 in our study, but often cited in the literature as important, was tested by ANOVA. No effects on seedling
25 size were detected, neither on aerial nor on subterranean parts.

26 27 28 **Discussion**

29
30 The most striking effect of environmental conditions on the development of beech saplings in our study
31 is the relationship between humus condition and sapling size (both aerial and subterranean parts), 5-

1 yr-old beech saplings being large only when A and OF horizons are rich in organic matter. Less striking
2 but apparent is the relationship between light conditions (incident light during the morning) and the
3 development of the rooting system, shallower rooting and lower rate of mycorrhization by *Cenococcum*
4 *geophilum* being associated with the occurrence of incident light during the morning, irrespective of
5 light conditions during the rest of the day.

6

7 In a study performed 20 years before on the same site, Pontailier (1979) found bigger 5-yr-old
8 saplings in open than in shade conditions. In our sample, no significant relationship is found between
9 canopy aperture and total light availability, and sapling size. Only incident light during morning hours
10 (until 10.30 AM, solar time) seems to have a relationship with the rooting system, in particular rooting
11 depth. On the other hand sapling size is strongly related to humus condition. Reasons for this apparent
12 discrepancy may be that Pontailier (1979) compared two nearby plots and thus did not sample saplings
13 over a wide environmental range.

14

15 Discrepancies between the results of correspondence analysis and analysis of variance with
16 respect to incremental growth of aerial parts in the first four years of sapling life may be due to strong
17 individual variations in the degree of caterpillar injuries. These parameters did not prove significantly
18 affected by humus condition, although they strongly contributed to the biomass of aerial parts, and
19 followed it along axis 1 of correspondence analysis (Fig. 1). The fact that the total biomass of aerial
20 parts was significantly affected by humus condition, together with stem increment of the 5th year,
21 indicates that regrowth during the 5th year smoothed out individual differences due to casual events.

22

23 Previous studies of the growth of beech seedlings and saplings under experimental conditions
24 mainly indicate importance of environmental factors associated with nutrition (Harley 1949; Harley &
25 Waid 1955; Garbaye 1983; van Praag et al. 1985): more nutrients and more light cause an increase in
26 dry weight, of both aerial and subterranean parts. Rather unexpectedly, we find bigger saplings in
27 places with lower biological activity in the A horizon (slower disappearance of humified organic matter).
28 We will, nevertheless, emphasize that no sapling was found in places with a well-developed OH
29 horizon (dysmoder humus form), i.e. at the lowest level of biological activity in the study site (Ponge &
30 Delhaye 1995). Our sample consists only of saplings growing in sites where beech usually regenerates
31 (cf. Koop & Hilgen 1987). When the substrate is very poor in clay minerals, as is the case in the study

1 area (Robin 1970), organic matter in the A horizon is likely to be the only possible site for nutrient and
2 water exchange, at least in the top 15 cm of the soil profile (Fardjah et al. 1980; Brady 1984).
3 Furthermore, soil organic matter may have a favourable effect on plant growth due to amelioration of
4 soil toxicity by complexation of heavy metals (Senesi et al. 1987), buffering capacity (James & Riha
5 1986) or sorption of toxic organic compounds (Stevenson 1994). Contrary to older individuals, whose
6 rooting systems may penetrate the soil down to the clayish B horizon (Pontailier 1979), the nutrient and
7 water requirements of seedlings and saplings can be satisfied in the A horizon. The dysmoder humus
8 form, characterized by the presence of a thick OH horizon (Brêthes et al. 1995), has been often
9 considered as a cause of beech regeneration failure (Weissen et al. 1986). Our results indicate that
10 hemimoder and eumoder humus forms, with thick OF horizon and dark A horizon but without or with
11 weakly developed OH horizon (Ponge & Delhay 1995), may be favourable to the development of
12 young beech saplings. In the study site, these humus forms are found in places with a thick sand layer
13 overlying limestone, oligomull (less favourable) being present when limestone comes nearer to the
14 surface.

15

16 Koop & Hilgen (1987) compared two plots on the same site of La Tillaie, one on oligomull (Plot
17 1), and another on moder or hemimoder humus (Plot 2). These authors did not study young beech
18 saplings, but observed that the thicket phase (old saplings with breast height diameter up to 12.5 cm)
19 was denser in Plot 1 than in Plot 2, which they attributed to strong competition by bracken (*Pteridium*
20 *aquilinum*) during the gap phase in the latter plot. Until more data are available on beech recruitment,
21 we hypothesize that within some limits (the absence of a dysmoder humus form) the stronger
22 development of saplings may compensate for site conditions less favourable for seedlings (and thus
23 with a lower rate of recruitment).

24

25 Our results give reason for questioning the importance of light for the development of beech
26 saplings. At a first look, our results may seem contradictory to results of previous studies (Teissier du
27 Cros et al. 1981), even in the same site (Pontailier 1979), which indicate a favourable effect of light on
28 seedling and sapling development and size. Given the well-known sensitivity of beech to air dryness
29 and changes in stomatal aperture during summer days (Salisbury & Ross 1985), the optimum of
30 photosynthesis may well occur during morning hours. This does not explain why beech saplings
31 growing under favourable light conditions have a shallower root system, a lower rate of mycorrhization

1 by *Cenococcum geophilum*, and lower resistance to infection diseases (deformation of root apices),
2 than those growing under less favourable light conditions. As a rule, a deep rooting system and high
3 resistance to infection are generally associated with efficient photosynthesis and good mycorrhization
4 (Harley & Waid 1955). However the black mycorrhizal ascomycete *Cenococcum geophilum* is more
5 resistant than other fungi to adverse conditions such as shading, chemical stress, drought or flooding
6 (Saleh-Rastin 1976; Meyer 1987). The strong development of this fungus on the sapling root system
7 when incident light does not come during morning hours can be explained both by physiological
8 drought (incident light during warmer hours or competition with trees for water), or shading (no or low
9 incident light). Signs of infection diseases (deformation of root apices) on saplings growing in better
10 light conditions (morning hours) could be associated with the absence or weaker development of
11 *Cenococcum geophilum*, the protective role of which against pathogens has been suspected by
12 several authors (Krywolap & Casida 1964; Grand & Ward 1969).

13

14

15 **Acknowledgements**

16

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18 (EGPN Committee), which is greatly acknowledged.

19

20

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- 10

1 **Table 1.** List of the 34 parameters used to describe the growth of aerial and subterranean parts of
 2 saplings during the past five years. Although interdependent, variations from year to year and lengths
 3 compared to diameters proved to be differentially affected by ecological factors.

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Code	Explanation
1	Dry weight of aerial parts (g.10 ⁻²)
2	Growth increment of aerial parts, 1 st year (mm)
3	Growth increment of aerial parts, 2 nd year (mm)
4	Growth increment of aerial parts, 3 rd year (mm)
5	Growth increment of aerial parts, 4 th year (mm)
6	Growth increment of aerial parts, 5 th year (mm)
7	Stem diameter, 1 st year shoot (mm)
8	Stem diameter, 2 nd year shoot (mm)
9	Stem diameter, 3 rd year shoot (mm)
10	Stem diameter, 4 th year shoot (mm)
11	Stem diameter, 5 th year shoot (mm)
12	Wounds by gypsy moth caterpillar, 1 st year shoot (1 or 0)
13	Wounds by gypsy moth caterpillar, 2 nd year shoot (1 or 0)
14	Wounds by gypsy moth caterpillar, 3 rd year shoot (1 or 0)
15	Wounds by gypsy moth caterpillar, 4 th year shoot (1 or 0)
16	Wounds by gypsy moth caterpillar, 5 th year shoot (1 or 0)
17	Total number of leaves
18	Mean thickness of leaves (µm)
19	Leaf wounds by gypsy moth caterpillar (1 or 0)
20	Number of branches produced during the 4 th year
21	Dry weight of subterranean parts (g.10 ⁻²)
22	Rooting depth (cm)
23	Maximum length of secondary roots between 0 and 3 cm depth (cm)
24	Maximum length of secondary roots between 3 and 6 cm depth (cm)
25	Maximum length of secondary roots between 6 and 9 cm depth (cm)
26	Maximum length of secondary roots between 9 and 12 cm depth (cm)
27	Maximum length of secondary roots between 12 and 15 cm depth (cm)
28	Maximum length of secondary roots between 15 and 18 cm depth (cm)
29	Maximum length of secondary roots between 18 and 21 cm depth (cm)
30	Maximum length of secondary roots between 21 and 24 cm depth (cm)
31	Total rate of mycorrhization (2, 1 or 0)
32	Rate of mycorrhization by <i>Cenococcum geophilum</i> (2, 1 or 0)
33	Deformation of apex (1 or 0)
34	Aerial/subterranean dry weight ratio

1 **Table 2.** List of the 23 parameters used to describe ecological conditions (litter and soil, canopy
 2 aperture and light) at places where saplings were collected.

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7 Code Explanation

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9	A	Thickness of the OL horizon (cm)
10	B	Thickness of the OF horizon (cm)
11	C	Thickness of the OH horizon (cm)
12	D	Munsell® colour of the A horizon at 3 cm depth
13	E	Munsell® colour of the A horizon at 6 cm depth
14	F	Munsell® colour of the A horizon at 9 cm depth
15	G	Munsell® value of the A horizon at 3 cm depth
16	H	Munsell® value of the A horizon at 6 cm depth
17	I	Munsell® value of the A horizon at 9 cm depth
18	J	Munsell® chroma of the A horizon at 3 cm depth
19	K	Munsell® chroma of the A horizon at 6 cm depth
20	L	Munsell® chroma of the A horizon at 9 cm depth
21	M	pH H ₂ O of the A horizon (top 5 cm)
22	N	Incident light coming from N-W direction (1 or 0)
23	O	Incident light coming from W direction (1 or 0)
24	P	Incident light coming from S-W direction (1 or 0)
25	Q	Incident light coming from S direction (1 or 0)
26	R	Incident light coming from S-E direction (1 or 0)
27	S	Incident light coming from E direction (1 or 0)
28	T	Incident light coming from N-E direction (1 or 0)
29	U	Total of N to T
30	V	Gap in the canopy (1 or 0)
31	W	Floor vegetation (1 or 0)

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1 **Table 3.** Relationship between organic matter content of A horizon and development of aerial and
 2 subterranean parts of beech saplings. Light A horizons (Munsell® value = 5 or 6) were compared with
 3 dark A horizons (Munsell® value = 3 or 4). Only significant relationships are shown. Means ± S.E. are
 4 given. P values refer to one-way ANOVA.

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7 8 9 10	Parameter	DARK A HORIZON (n = 21)	LIGHT A HORIZON (n = 20)	P value
11	Biomass of aerial parts	38±5 g.10 ⁻²	26±4 g.10 ⁻²	0.045
12	Growth increment of aerial parts, 5 th year	59±12 mm	28±4 mm	0.022
13	Stem diameter, 2 nd year shoot	1.9±0.1 mm	1.5±0.1 mm	0.035
14	Stem diameter, 3 rd year shoot	1.5±0.1 mm	1.2±0.1 mm	0.005
15	Stem diameter, 4 th year shoot	1.3±0.0 mm	1.0±0.1 mm	0.034
16	Total number of leaves	15±2	11±1	0.022
17	Biomass of subterranean parts	47±6 g.10 ⁻²	30±4 g.10 ⁻²	0.022
18	Rooting depth	18±1 cm	15±1 cm	0.006
19	Max. length of secondary roots 18 to 21 cm depth	0.7±0.3 cm	0.1±0.0 cm	0.016

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29 **Table 4.** Influence of incident light during morning (coming from S-E) on development of aerial and
 30 subterranean parts of beech saplings. Only significant relationships are shown. Means ± S.E. are
 31 given. P values refer to one-way ANOVA.

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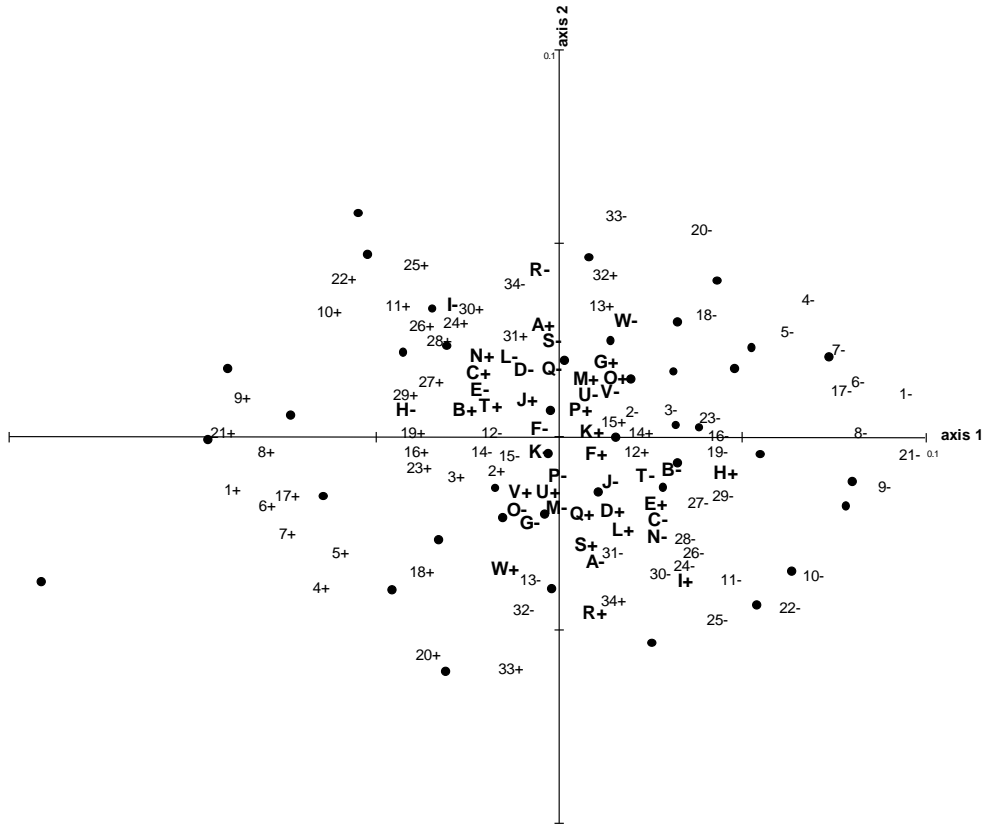
34 35 36	Parameter	NO LIGHT FROM SE	LIGHT FROM SE	P value
37	Rooting depth	19±1 cm	14±1 cm	0.0002(***)
38	Max. length of secondary roots 15 to 18 cm depth	1.4±0.4 cm	0.1±0.1 cm	0.020(*)
39	Max. length of secondary roots 18 to 21 cm depth	0.6±0.2 cm	0.1±0.1 cm	0.045(*)
40	Rate of mycorrhization by <i>Cenococcum geophilum</i>	0.8±0.1	0.2±0.1	0.007(**)
41	Deformation of apex	0.1±0.1	0.4±0.1	0.033(*)

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LEGENDS OF FIGURES

Fig. 1. Correspondence analysis. Projection in the plane of the first two axes (26 and 8% of total variance, respectively). The 41 seedlings are indicated by black dots, the active variables (34 x 2 morphological variables) by numbers according to Table 1, and the passive variables (23 environmental parameters) by letters according to Table 2. Plus or minus symbol following a number or a letter indicates the pole for higher and lower values, respectively. Variance and mean were fixed to 1 and 10 for all variables, respectively.



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2 Fig. 1