Morphometric variability in *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 in relation to humus type and season

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SUMMARY

Intraspecific variability was studied in *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 with the help of a Benzecri's factorial analysis of correspondences. Body shape and size can vary according to the type of humus in which the nematodes are living. Two morphometric characters (body and tail lengths) can be used to distinguish populations, thus like the other mononch *Prionchulus punctatus, Clarkus papillatus* can be considered as a good indicator of humus type differentiation. A seasonal variability also was demonstrated in several biotopes representative of each investigated humus type. Environmental and nutritional influences upon morphometric characters have been discussed.

RÉSUMÉ

Variabilité morphométrique de Clarkus papillatus *(Bastian, 1865) Jairajpuri, 1970 en relation avec les types d'humus et les saisons*

La variabilité intra-spécifique de *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 a été étudiée à l'aide d'une analyse factorielle des correspondances de Benzécri. La forme et la taille du corps varient en fonction du type d'humus dans lequel vivent les animaux. Deux paramètres mesurables (taille du corps et de la queue) peuvent être utilisés pour séparer les populations. *Clarkus papillatus,* tout comme *Prionchulus punctatus,* peut donc être considéré comme un bon indicateur pédobiologique. De plus, une variabilité saisonnière a été démontrée dans différents biotopes représentatifs de chacun des types d'humus prospectés. Les auteurs discutent de l'influence de l'environnement et des facteurs nutritionnels sur les caractères morphométriques.

During our investigations on mononchid nematodes in different forest humus near Paris (Arpin, 1979; Arpin *et al.*, 1984*a*, 1984*b*; Arpin & Ponge, 1984; Samsœn *et al.*, 1984), the intraspecific variability of *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 was analysed. This species is common in all soils, nevertheless it prefers fresh soils with an acid mull humus and a thick litter layer (Arpin, 1985). Besides an evident interest for systematics, the short-term objective of this study is to find good species, which may indicate, by their morphotypes, pedobiological influences.

Materials and methods

The same material was used in this study as by Arpin (1979), with the following classification :

— Mor : Four biotopes, 120 individuals (Fontainebleau forest).

— Moder : Three biotopes, 60 individuals (Fontainebleau and Sénart forests).

— Acid mull : Four biotopes, 378 individuals (Sénart and Armainvilliers forests).

— Eutrophic mull : One biotope, 111 individuals (Sénart forest).

— Calcic mull : Five biotopes, 164 individuals (Fontainebleau forest and Laboratory Park at Brunoy).

The latter type of humus we subdivided into calcic hydro-mull (one biotope, 52 individuals) and well-drained and aerated calcic mull (four biotopes, 112 individuals).

Definition and characterization of the different humus types follow the European classification (Duchaufour, 1977). Chemical analysis were performed at Laboratory of Soil Science, ORSTOM, Bondy, France.

The nematodes were heat-killed and fixed with 4 % formaldehyde and mounted in pure glycerin. Measurements of 833 females were made from drawings under a Leitz microscope with camera lucida. Measurement data were analysed using Benzecri's analysis of correspondences which is a powerful technique for displaying

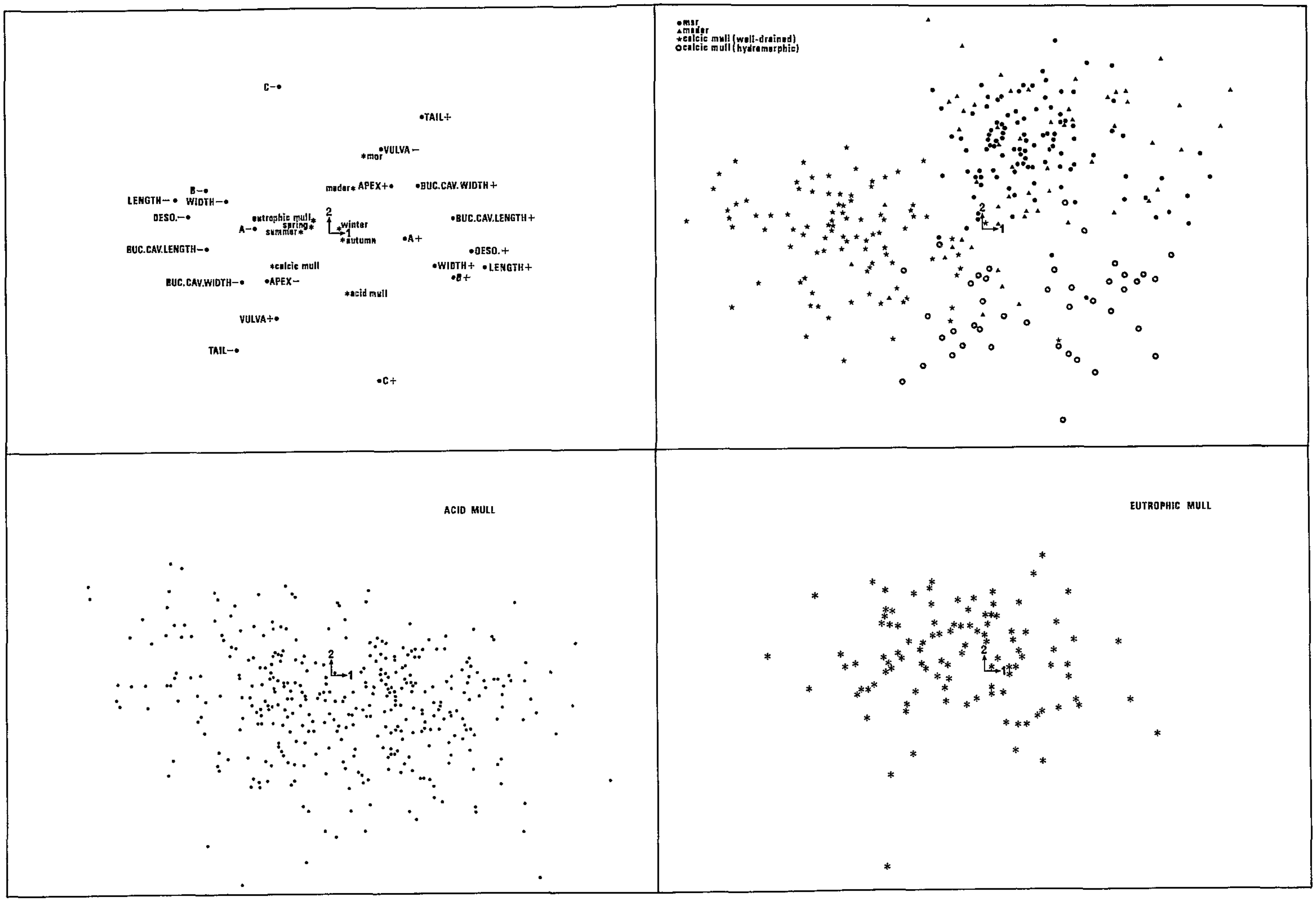

Fig. 1. Correspondence analysis. Projection of 833 individuals and 22 variates in the plane of the first two axes. Variates and animals corresponding to each humus type have been separately represented in order to make clearer the relations between humus type and factorial 1- and 2- coordinates. Additional variates coded as 1 or 2 (not involved in the analysis) have been placed on the graph and are indicated by a star symbol.

Table 1

Biometrics of *Clarkus papillatus* (means with confidence intervals x ± $t_{0.05}$ S_x) for each humus type (For each couple of variates distinct letters after the mean indicate a significant difference)

	Mor	*Moder*	*Acid mull*	*Brown-earth mull*	*Calcic mull (well-drained)*	*Calcic mull (hydromorphic)*
Length (mm)	1.276 ± 0.013 *c*	1.277 ± 0.023 *bc*	1.275 ± 0.011 *c*	1.242 ± 0.015 *b*	1.136 ± 0.014 *a*	1.355 ± 0.024 *d*
Width (µm)	49.69 ± 0.69 *b*	50.72 ± 0.98 *b*	50.21 ± 0.37 *b*	51.41 ± 0.77 *c*	46.78 ± 0.63 *a*	52.35 ± 0.99 *cb*
Œsophagus (µm)	351.49 ± 2.75 *c*	355.33 ± 4.56 *c*	350.36 ± 1.92 *c*	343.60 ± 2.63 *b*	322.84 ± 2.50 *a*	359.42 ± 4.77 *c*
Vulva (%)	61.15 ± 0.18 *a*	61.21 ± 0.34 *a*	62.04 ± 0.12 *b*	61.49 ± 0.24 *a*	62.32 ± 0.24 *b*	62.36 ± 0.35 *b*
Tail (µm)	85.96 ± 0.99 *d*	84.98 ± 2.10 *d*	76.08 ± 0.61 *b*	79.65 ± 1.01 *c*	72.78 ± 1.06 *a*	75.83 ± 1.87 *b*
A	25.78 ± 0.26 *b*	25.25 ± 0.45 *b*	25.44 ± 0.18 *b*	24.23 ± 0.24 *a*	24.35 ± 0.26 *a*	25.95 ± 0.43 *b*
B	3.63 ± 0.02 *b*	3.60 ± 0.03 *b*	3.64 ± 0.02 *b*	3.62 ± 0.02 *b*	3.52 ± 0.03 *a*	3.77 ± 0.03 *c*
C	14.88 ± 0.16 *a*	15.11 ± 0.32 *a*	16.82 ± 0.14 *c*	15.65 ± 0.23 *b*	15.65 ± 0.20 *b*	17.95 ± 0.33 *d*
Buc. cav. length (µm)	27.46 ± 0.14 *d*	27.75 ± 0.26 *d*	26.62 ± 0.12 *c*	25.61 ± 0.14 *b*	25.24 ± 0.17 *a*	26.68 ± 0.28 *c*
Buc. cav. width (µm)	15.08 ± 0.13 *d*	15.12 ± 0.19 *d*	14.39 ± 0.07 *c*	14.08 ± 0.12 *b*	13.58 ± 0.12 *a*	13.99 ± 0.16 *b*
Apex (%)	84.58 ± 0.21 *b*	84.06 ± 0.33 *a*	83.93 ± 0.13 *a*	83.71 ± 0.22 *a*	83.41 ± 0.21 *a*	83.32 ± 0.36 *a*

structure in complex two-way tables of data (Lebart, Morineau & Fenelon, 1979; Greenacre, 1984). The variates included in the analysis are listed in Table 1. Coding and transformation of the data were explained previously (Arpin *et al.*, 1984*a*).

Results

Influence of humus type

Figure 1 shows the repartition of animals (833 females) and measurement variates (11 duplicate items) along the 1st and 2nd axes. The different humus types have been separately represented in order to make the graphs more readable.

Axis 1 is related to general size of the body, with the characters LENGTH (body length) and OESO. (œsophagus length) more tied to it, and also to a lesser extent BUC.CAV.LENGTH (buccal cavity length), WIDTH (body width at œsophagus end) and the b ratio (body length divided by œsophagus length). Axis 2 is related to the relative tail development, with the variates TAIL (tail length), c ratio (body length divided by tail length) and to a lesser extent VULVA (vulva position).

In the plane of the 1- and 2-axes (Fig. 1), we can see that the most characterized populations are those providing from acid soils (mor and moder humus as a whole). These two humus types are not separable, both having positive 1- and 2- coordinates. Tail size rather than vulva position is largely responsible for this phenomenon. We can say that mor- or moder-inhabiting individuals are in average of a greater size, and with a (relatively) long tail (small c ratio) and an anteriorly situated vulva. Acid mull individual points are scattered in the plane but, in average, the corresponding animals have a rather short tail as compared to the mor- and moder-animals. Eutrophic mull animals are significantly shorter, having negative coordinates along the axis 1 whereas calcic mull animals are characterized by their short tail (negative coordinates along the axis 2). This latter group must be divided into two subgroups, hydromorphic calcic mull (alder grove at Brunoy) being represented by larger animals (positive coordinates along the axis 1) and the well-drained calcic mull with smaller nematodes (negative coordinates along the axis 1).

Table 1 summarizes the measurements made in each humus type. With the help of correspondences analysis we find that the bulk of intra-specific variability (57 % of the whole variance extracted by the 1- and 2-axes) is related to humus type. Two characters, namely body and tail length, are more closely related respectively to the first and second axis. So we have represented in Figure 2 their mean measurements in each humus type or sub-

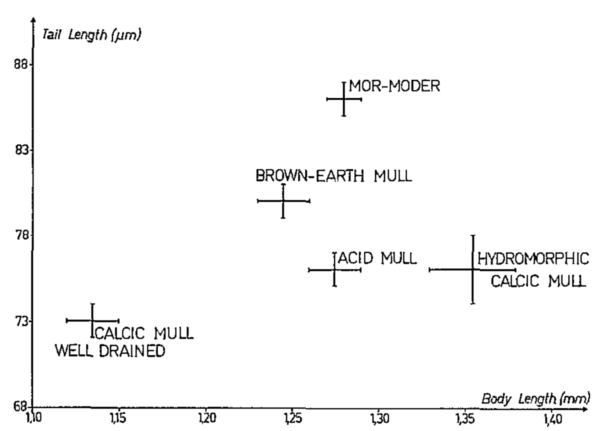

Fig. 2. Mean (with confidence interval ± $t_{0.05}$ S_x) tail and body length of *Clarkus papillatus* populations for each humus type.

Table 2

Biometrics of *Clarkus papillatus* (means with confidence intervals $xt_{0.05}\,S_x$)
for each season and one biotope representative of each humus type
(mor and well-drained calcic mull excluded, due to the lack of some seasons)

	Moder			*Calcic hydro-mull*		*Brown-earth mull*			*Acid mull*			
Individuals	*Winter* 12	*Spring* 14	*Autumn* 11	*Winter* 30	*Autumn* 19	*Winter* 39	*Spring* 15	*Autumn* 51	*Spring* 12	*Summer* 22	*Autumn* 82	*Winter* 49
Length (mm)	1.368 ± 0,044	1.244 ± 0.029	1.201 ± 0.046	1.371 ± 0.027	1.342 ± 0.047	1.291 ± 0.022	1.267 ± 0.027	1.207 ± 0.019	1.244 ± 0.069	1.154 ± 0.047	1.308 ± 0.020	1.303 ± 0.036
Width (μm)	51.33 ± 1.10	51.64 ± 1.72	46.36 ± 1.63	53.530 ± 1.00	50.74 ± 1.95	54.62 ± 1.15	50.53 ± 2.02	49.41 ± 0.87	50.08 ± 2.79	49.36 ± 1.89	50.77 ± 0.78	51.24 ± 1.07
Œsophagus (μm)	373.33 ± 9.04	348.57 ± 7.42	345.45 ± 8.58	362.67 ± 5.45	357.37 ± 9.44	352.05 ± 4.20	346.67 ± 6.80	336.86 ± 3.26	344.17 ± 10.90	331.36 ± 8.21	357.07 ± 3.70	356.12 ± 5.83
Vulva (%)	60.40 ± 0.53	62.47 ± 0.68	60.46 ± 0.52	62.40 ± 0.42	62.55 ± 0.43	61.32 ± 0.40	61.35 ± 0.60	61.60 ± 0.37	62.09 ± 1.21	62.22 ± 0.35	62.00 ± 0.26	62.40 ± 0.40
Tail (μm)	91.50 ± 4.42	74.64 ± 1.65	88.09 ± 2.58	77.90 ± 1.86	72.26 ± 3.83	81.05 ± 1.56	80.73 ± 2.39	78.55 ± 1.61	74.08 ± 3.09	73.41 ± 2.82	78.29 ± 1.03	76.37 ± 1.61
A	26.66 ± 0.54	24.14 ± 0.78	25.93 ± 0.89	25.63 ± 0.49	26.55 ± 0.86	23.68 ± 0.35	25.22 ± 0.67	24.45 ± 0.34	24.80 ± 0.75	23.50 ± 0.87	25.83 ± 0.36	25.44 ± 0.51
B	3.68 ± 0.07	3.57 ± 0.05	3.48 ± 0.06	3.78 ± 0.04	3.75 ± 0.05	3.67 ± 0.03	3.67 ± 0.05	3.58 ± 0.04	3.62 ± 0.11	3.48 ± 0.06	3.66 ± 0.03	3.66 ± 0.05
C	14.99 ± 0.54	16.64 ± 0.39	13.64 ± 0.39	17.64 ± 0.26	18.66 ± 0.69	15.98 ± 0.36	15.79 ± 0.67	15.42 ± 0.36	16.85 ± 1.02	15.79 ± 0.52	16.77 ± 0.29	17.10 ± 0.39
Buc. cav. length (μm)	28.78 ± 0.38	26.89 ± 0.36	28.1[illegible] ± 0.39	26.29 ± 0.33	27.31 ± 0.38	25.61 ± 0.24	26.19 ± 0.35	25.47 ± 0.19	26.49 ± 0.78	25.95 ± 0.46	27.16 ± 0.27	26.90 ± 0.35
Buc. cav. width (μm)	15.59 ± 0.39	14.48 ± 0.17	15.23 ± 0.26	13.75 ± 0.15	14.44 ± 0.24	14.19 ± 0.25	14.41 ± 0.26	13.85 ± 0.12	14.35 ± 0.40	14.39 ± 0.33	14.64 ± 0.16	14.63 ± 0.20
Apex (%)	84.92 ± 0.73	83.82 ± 0.62	84.33 ± 0.79	83.32 ± 0.52	83.44 ± 0.60	84.01 ± 0.36	83.93 ± 0.64	83.50 ± 0.27	83.91 ± 0.52	83.90 ± 0.48	84.45 ± 0.22	84.17 ± 0.34

type with confidence intervals. A clear separation can be made between the different humus types but we must point out that this separation is proportionally better when there are more individuals in the compared groups.

Influence of season

On Figure 1 we can see that the four season-points (each season was projected as a supplementary variate not involved in the analysis, coded as 1 or 0) are separated in two groups along the axis 1. In this way autumn and winter (positive coordinates, large animals) are opposite to spring and summer (negative coordinates, small animals). So seasonal influences interfere with humus type influences, and at first glance make doubtful the previous results. Since some stands have no or fewer animals in a given season, we have a bias in establishing the means relative to each humus type. Mononchida are known to be very sensitive to soil dryness during summer months, so the number of collected animals may be in some cases very small and only composed of larval stages (Arpin, 1985).

Since autumn is the only season where the number of animals is such high as to make valid comparisons between populations, these individuals were separately analysed (Fig. 3). The results seem to be identical to previous analysis (Fig. 1). Therefore season-induced morphometric variability does not hide humus type influence and we are now confident that the structure described by figure 1 is not an artefact.

In order to study more accurately seasonal influences we have analysed separately four sites where *Clarkus papillatus* is well-represented all over the year. These are the moder from Sénart forest (39 individuals), the calcic hydromull from Brunoy (52 individuals), the acid mull from Armainvilliers forest (165 individuals) and the eutrophic mull from Bois de la Tour (111 individuals). Table 2 gives mean measurement data for each site and season (seasons with less than ten individuals were excluded from this table but not from the analysis).

In the Sénart moder (Fig. 4 *a*), the plane of axes 1 and 2 separates three groups which correspond to autumn, spring and winter. Summer is represented only by two points far from each other, so for this season factorial analysis gives poor indications. Autumn animals are of small size (small body length, body width and œsophagus length) and have a small c ratio, so their tail is proportionally of great size. Winter animals are larger; they have a large buccal cavity and a long tail. Their a and b ratios are large, so they are relatively thinner and with a short œsophagus. Spring animals are small, with a small buccal cavity; their c ratio is large and on the contrary their a ratio is small. So they are relatively thick and short-tailed. They are also characterized by a slightly posteriorly placed vulva. The best separation is given by plotting together body length and tail length (Fig. 4 *b*). Briefly we can say the winter animals are bigger than the autumn ones, these two groups being distinguished from spring animals by their long tail.

In the hydromorphic calcic mull (Fig. 5), we can distinguish two groups, winter and autumn, which are separated by axis 2. Axis 1 may be interpreted as a size factor which opposes small to great animals at the inside of the two groups evidenced by axis 2. This last axis is tightly related to c ratio. So autumn animals are relatively short-tailed as compared to winter animals. To a lesser extent they have also a greater buccal cavity and a slenderer body. Nevertheless it seems impossible to find measurable criteria in order to have a clear separation between these two groups.

In the eutrophic mull (Fig. 6 *a*), axis 1 opposes winter animals (large body length and width) to autumn animals (small size). Spring animals do not form a distinct

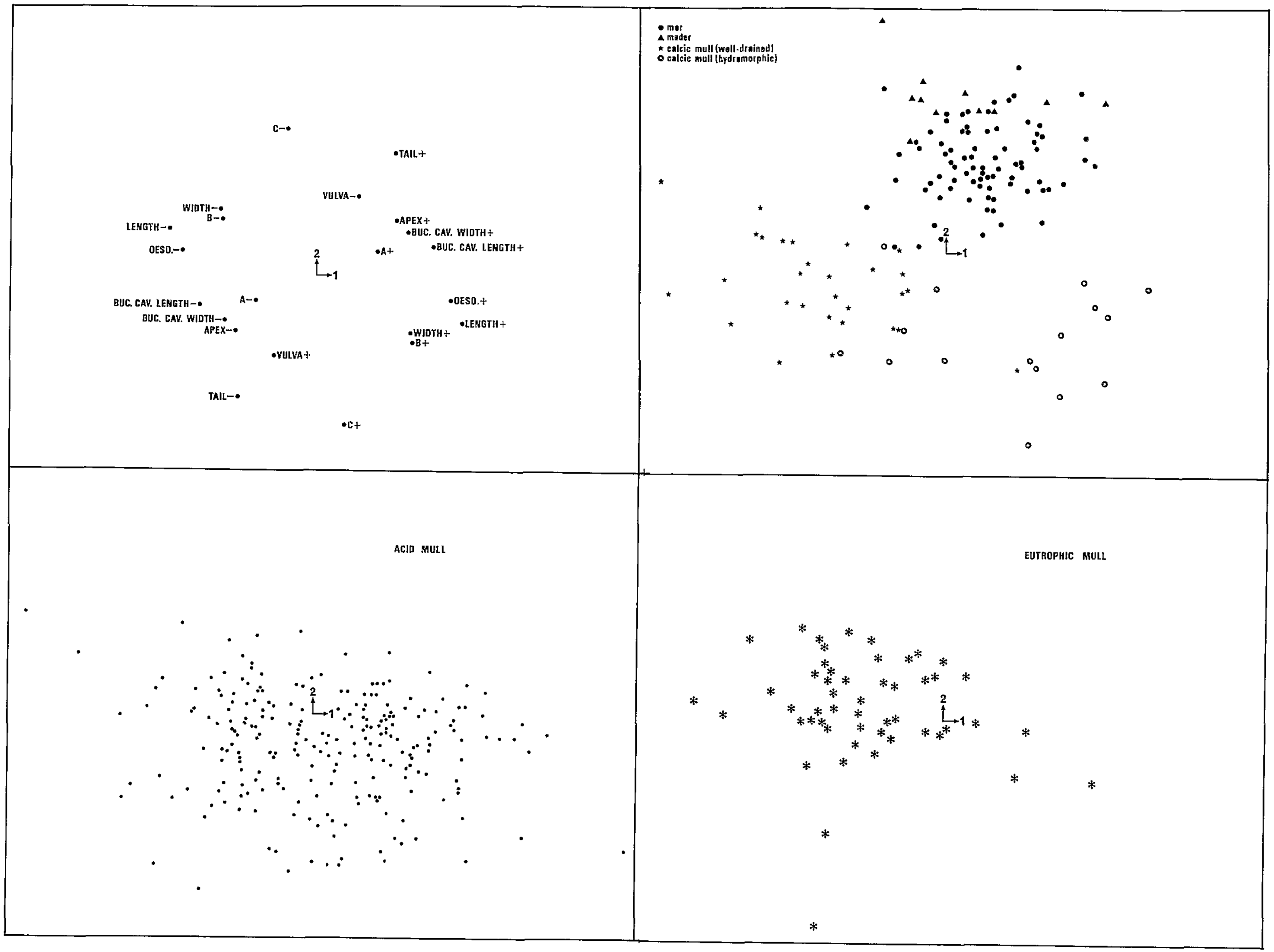

Fig. 3. Correspondence analysis. Projection of 422 autumn individuals and 22 variates in the plane of the first two axes. Partial projection of each humus type as in Fig. 1.

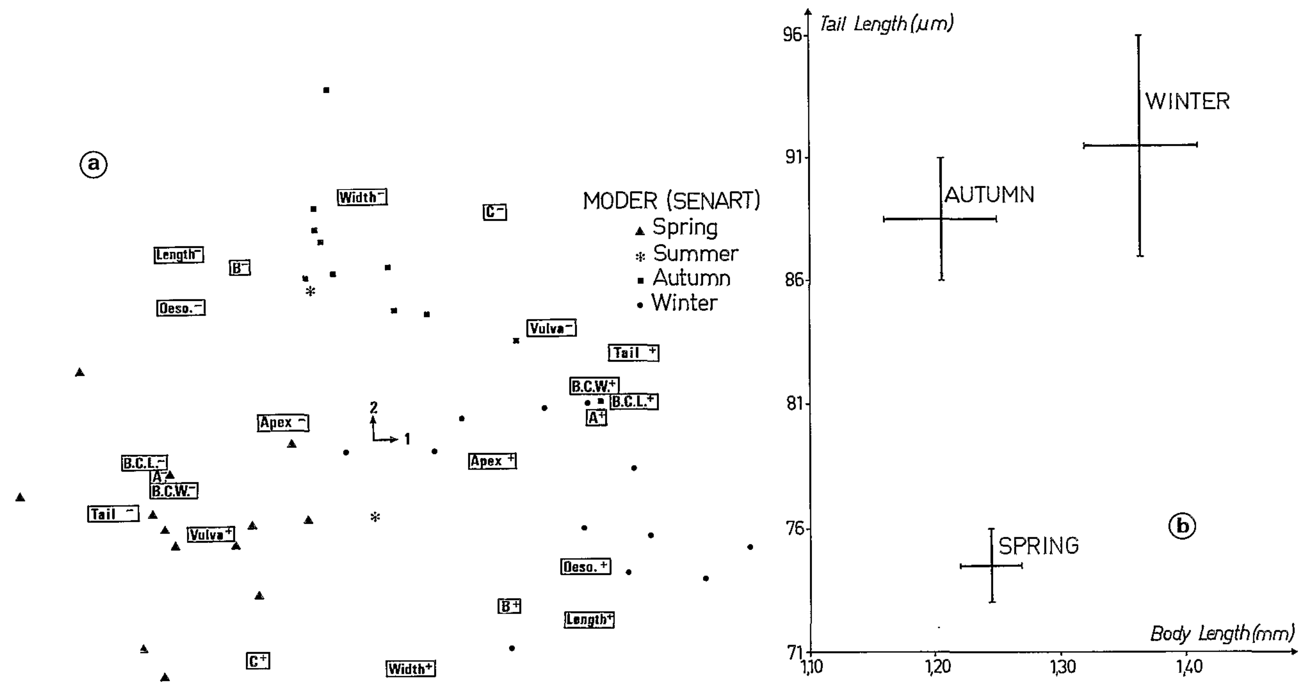

Fig. 4. Sénart moder. A : Correspondence analysis, simultaneous projection of 22 variates and 39 individuals in the plane of the first two axes, influence of season; B : Mean (with confidence interval) tail and body length for each season.

group but they are in an intermediate position along axis 1 and all have negative coordinates along axis 2 (long tail and slender body). Plotting couples of characters

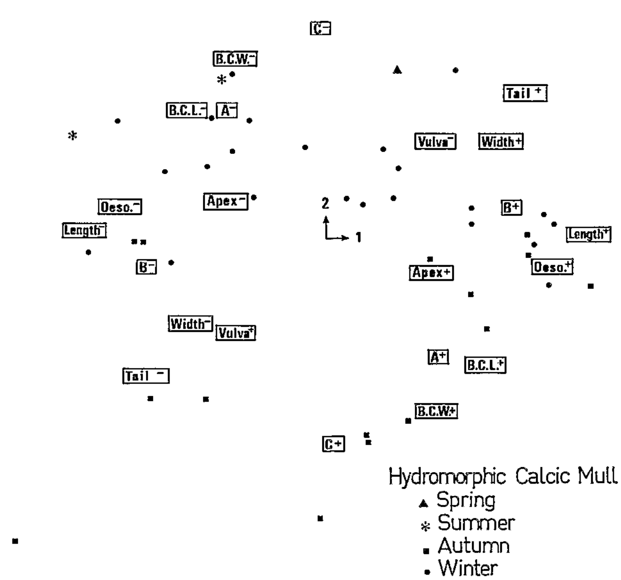

Fig. 5. Hydromorphic calcic mull (Brunoy). Correspondence analysis. Simultaneous projection of 22 variates and 52 individuals in the plane of the first two axes. Influence of season.

(Fig. 6 *b*: body length/body width; Fig. 6 *c*: buccal cavity length/buccal cavity width) gives a good separation between the three seasons.

In the acid mull (Fig. 7) seasonal differences are badly expressed by morphology. Axis 1 is a size gradient, larger animals having also larger a and b ratio (slender body and short œsophagus). Axis 2 is related to tail development and, to a lesser extent, to vulva position. In general autumn and winter animals are longer and slenderer than spring and summer ones, but tail relative dimension does not seem to be correlated to season in this stand.

Discussion

When we compare these results with those previously obtained for *Prionchulus punctatus* (Arpin & Ponge, 1984), where tail and body lengths were also two good criteria for determining humus type influences, we can notice some similarities. Acid humus is in both cases inhabited by large animals which have a relatively long tail; on the contrary, calcic mull animals are smaller with a short tail. Nevertheless in this last humus type we can now separate hydromorphic (long animals) from well-drained sites (short animals), which was not possible with *Prionchulus punctatus*. Concerning calcic mull humus the only criterion which is good for both *Clarkus papillatus* and *Prionchulus punctatus* is the short tail.

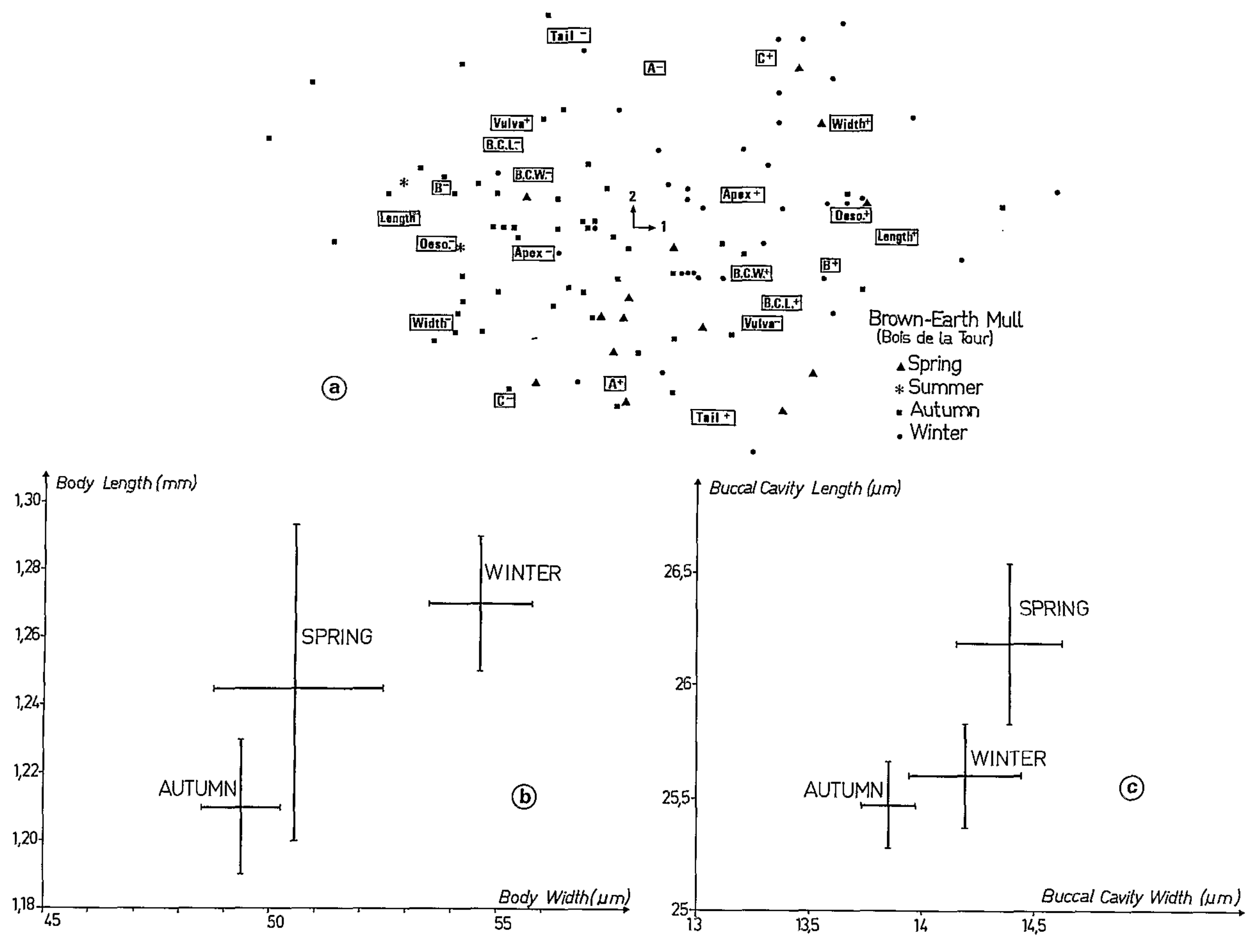

Fig. 6. Brown-earth mull (Bois de la Tour). A : Correspondence analysis, simultaneous projection of 22 variates and 111 individuals in the plane of the first two axes, influence of season; B : Mean (with confidence interval) body length and body width for each season; C : Mean (with confidence interval) buccal cavity length and width for each season.

When we consider results as a whole it seems that, contrary to humus type, season differentially influences morphometric characters. For instance, in the hydromorphic calcic mull, the autumnal populations are smaller than winter ones but possess a larger buccal cavity; for brown-earth mull, the winter ones are larger but spring populations have a greater buccal cavity; in moder humus, autumn individuals possess larger tail and buccal cavity and a higher placed dorsal tooth apex than spring ones which however have a greater body length (Tab. 2).

From these different results we can think that the research of the factors responsible for such a variation in the morphometric characters of entire nematode populations is complicated. Then we can only speculate that influence of humus type may be the result of purely physico-chemical effects (acidity, cation exchange capacity, carbon dioxyde buffering, etc.) or may be related to alimentary resources. For instance, *Clarkus papillatus*, although a predatory nematode, has a varied diet, ingesting bacteria and clay minerals beside animal prey (Arpin, 1976; Arpin & Kilbertus, 1981; Saur, 1986). These studies show that mull-inhabiting animals ingest clay minerals unlike mor- or moder-inhabiting animals. Moreover, quality and quantity of nutriments vary throughout the year : Saur's work (1986) gives evidence of successive diets during the year, by observing ingested food in the intestine of nematodes with the help of transmission electron microscopy. Animal prey are rather ingested in autumn and replaced by a bacterial diet in spring. In our work we observe generally that spring or summer populations are smaller than autumn or winter ones. To determine to what extent feeding habits influence morphology further experiments are needed but with respect to this problem several other works are notable : they concern laboratory cultures of free-living Rhabditida or Tylenchida. For example, in field experiment with enrichment material (fungus) Sohlenius

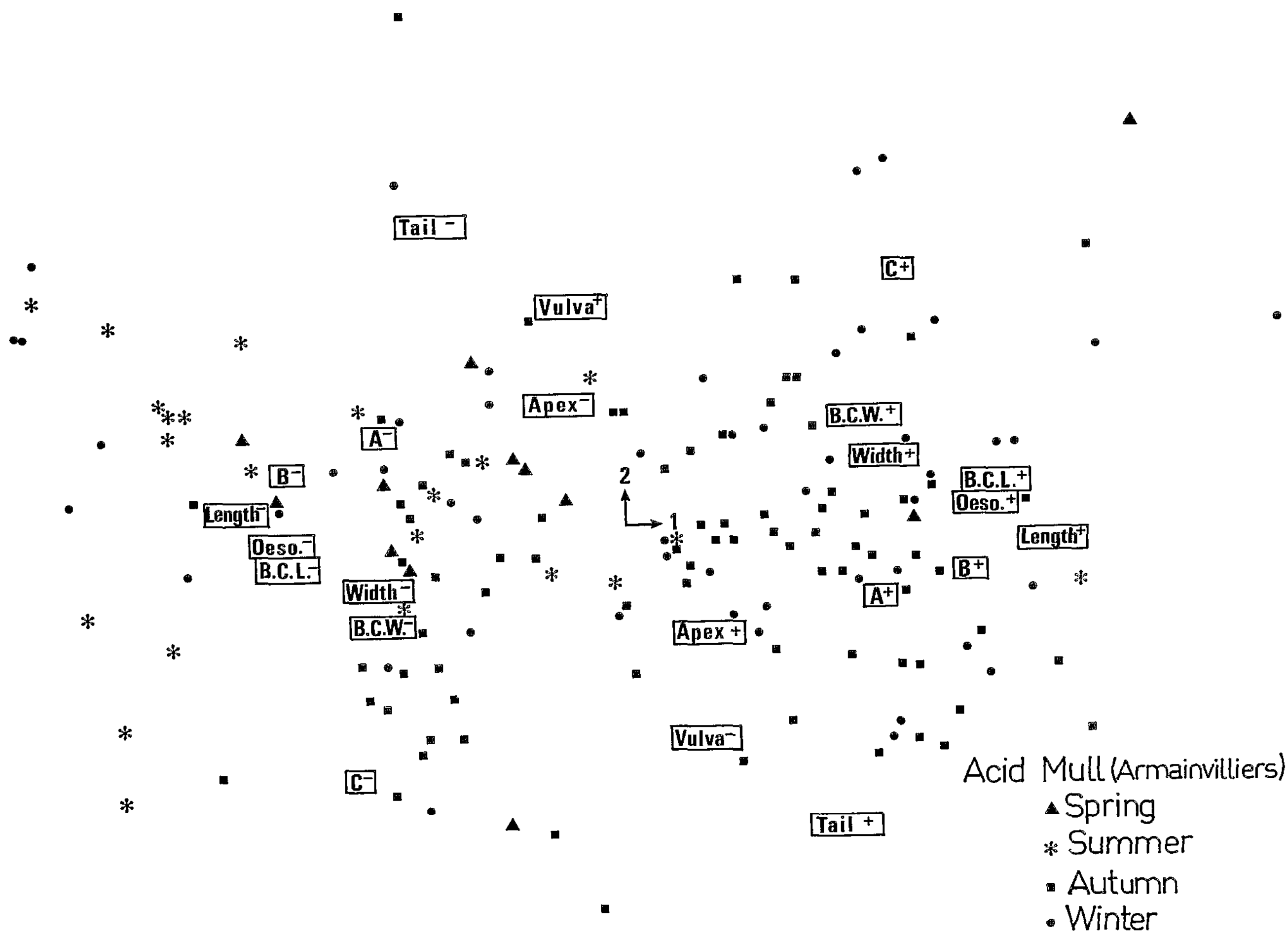

Fig. 7. Armainvilliers acid mull. Correspondence analysis. Simultaneous projection of 22 variates and 165 individuals in the plane of the first two axes. Influence of season.

(1973) has shown that the length of *Acrobeloides nanus* is highly variable : 382.3 µm in the untreated soil, 437.5 µm at the inside of the enriched plot eight days after application and from 420.1 µm to 400.3 µm in the surrounding soil 16 to 35 days after application. Geraert (1983) demonstrated that *Mesodiplogaster pseudolheritieri* in bad cultures has a body length from 630 to 855 µm and a tail length from 123 to 175 µm; in good cultures body length varies from 770 to 2 130 µm and tail length from 125 to 228 µm; but it is specified that, if all individuals in good cultures are larger, nevertheless the vulva position does not vary between these two cultures (in our work we observe the same phenomenon). *Aphelenchus avenae* populations are concerned by the host on which they feed : on Potato Dextrose Agar (with different fungi) individual sizes vary from 911 µm at 14 days to 788 µm at 21 days and 785 µm at 56 days after inoculation; on *Rhizoctonia* medium individual sizes are respectively 991, 844 and 788 µm. An interesting work using multivariate analysis (Townshend & Blackith, 1975) has shown that there are relationships between morphometry of *Aphelenchus avenae* and its fungal diet; the two first principal components refer to size and robustness (width) : longer nematodes came from fungi on which large populations had developped while shorter nematodes came from cultures bearing small populations. Moreover longer nematodes were slimmer in appearance than shorter ones; this observation is similar to our own : mor and moder humus populations are larger than calcic mull ones but they have a lesser width. After having observed morphological variations between different populations of the mononch *Iotonchus parazschokkei*, Clark (1963) put the hypothesis of a causal relationship involving the availability of food in the different localities where this species was recorded; the smallest specimens came from soils of extremely low fertility (two localities) and in both these two cases the amount of nematodes was very low.

These last results are all the more conclusive as populations show only a limited amount of variation in each locality.

Physico-chemical influences may also be discussed, particularly regarding temperature and humidity. In Figure 8 is displayed the relation between temperature and pF at the sampling date, in each stand which was chosen for factorial analysis. Although measurements were punctual we can see that the more distinct are the environmental conditions the more segregated are the corresponding seasonal clusters in factorial charts. This is particularly true for Sénart moder (Fig. 4 A) and alder calcic hydro-mull (Fig. 5). On the contrary eutrophic mull from Bois de la Tour (Fig. 6 A) and still more Armainvilliers acid mull (Fig. 7) have more stable environmental conditions, so a lesser extent of morphological variation along the year. These two last biotopes are also those were *Clarkus papillatus* is more abundantly encountered in any season.

We are aware of the causal relationships between soil physico-chemical factors and microbial activity from which some difficulties arise when nutritional influences have to be isolated. However a laboratory study by Popovici (1973) proved that temperature can influence *Cephalobus nanus* morphometry independantly from culture medium : a decrease of body length when temperature increases was noted. The same conclusion is formulated by Sohlenius (1968) for *Rhabditis terricola.* However for *Aphelenchus avenae,* Evans and Fisher (1970) related a decreasing length to an increasing temperature that induces a greater reproduction rate and consequently a decrease in the amount of available food. In our own work spring and summer acid mull populations are smaller than autumn and winter ones with temperature varying respectively from 14-16° to 6° (Fig. 8); but in the case of these field populations the

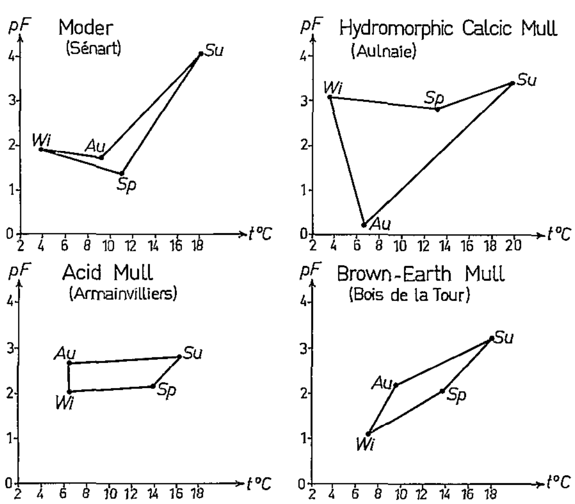

Fig. 8. Relation between temperature and pF at the sampling time in the four humus types selected for multivariate analysis.

food diet is not the same all along the year. Also it must be noticed that spring moder and brownearth mull populations are smaller than winter ones (Tab. 2).

As it has been demonstrated by Anderson and Coleman (1982) and Sohlenius (1985) from multispecific breeding experiments at controlled temperatures, the problem of niche specificity and species cohabitation is related to distinct adaptations of individual species. Although further experiments are needed to, we can speculate that morphometric variations related to humus type and season are relevant to the same ecological problem : how Nematoda can adapt themselves in view of taking better advantage of their environment.

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