Preliminary observations on oribatid mites of riparian soils in Uruguay

by M. Sarasola¹, H. Vera¹, G. Wauthy² & M. Dufrêne³

- ¹ Ecologia, Universidad de la República, Facultad de Ciencias, Calle Tristán Narvaja 1674, 11200 Montevideo, Uruguay.
- ² Département d'Entomologie, Institut royal des Sciences Naturelles de Belgique, rue Vautier 29, B-1040 Bruxelles, Belgique.
- ³ Unité d'Écologie et de Biogéographie, Place Croix du Sud 5, B-1348 Louvain-la-Neuve, Belgique.

Abstract

The aim of this paper is to compare, six months before flooding and three weeks after flooding, the oribatid assemblages living in riparian forest and grassland ecosystems in Uruguay. Both sampling sites were located in the flood plain and their oribatid assemblages were surveyed in spring 1989 and autumn 1990. Species richness and diversity (H') of assemblages were different in both sampling stands. In addition, their numerical structure changed more markedly between the two sampling occasions in the forest than in the grassland. Finally, we discuss assumptions to explain both the weak density of oribatids in the site studied and the relative weakness shown by South American genera within the local assemblages.

Introduction

One of the major concerns of ecology is understanding the distribution and abundance of species. Yet, although oribatid mites (as well as collembolans) are the most diverse group of soil arthropods, knowledge of their distribution and abundance in South America still is very incomplete. In Uruguay, riparian forests are the most important natural wooded area that occupies nearly $9,10^5$ ha (3% of the country's total area; CARRERE, 1989). As a result of heavy rains, riparian forests experience, in general from May to September, two or three periods of flooding which can last two or three weeks. The consequence is that riparian forests are broad alluvial areas which can be regarded as ecotones between aquatic and upland ecosystems with peculiar vegetation and soil.

This paper is a preliminary contribution to the study of soil oribatid

mites living in riparian ecosystems in Uruguay. Its aim is to compare, before and after flooding, the numerical structure of oribatid assemblages in two distinct sites, a wood and a prairie, alongside the Rio Negro river.

Materials and methods

In this study, the sampling area was selected in a site undisturbed by human activities (neither sylviculture nor farming nor mowing) and located (Fig. 1) about 30 km west of the confluence of Tacuarembo and Rio Negro rivers ($32^{\circ} 22'$ S; $54^{\circ} 11'$ W) and approximately in the centre of the geomorphological area known as the Sedimentary Undulating region (DU-RAN, 1985) within the Pampas region (sensu Good, 1964).

The forest stand was both floristically and structurally complex, and was comprised of several canopy trees, Allophyllus edulis, Blepharocalyx tweediei, Eugenia uniflora, Pouteria salicifolia, Rupretchia salicifolia, Sapium sp., Sebastiania brasilensis and Sebastiania klotzschiana, growing above a shrub cover and a herbaceous stratum. Organic horizons of the soil were of the mull type. The litter layer (Ol sensu DELECOUR, 1980) was always thin (<0.5 cm) and discontinuous. In contrast, the thickness of both the Of and Ah1 horizons varied during the year, with a minimum in spring and a maximum in autumn (0.5 to 1.5 cm for the Of layer; 1.5 to 5 cm for the Ah1 layer).

The nearby grassland stand was also located in the flood plain. The herbaceous cover included Axonopus sp., Paspalum sp. and Oxalis sp. in spring and autumn, and Eryngium sp. in spring only. The mull soil consisted of a very thin litter layer and a thick (>30 cm) Ah horizon where no subhorizon was detectable at any time.

Oribatid populations of each stand were surveyed on two occasions, in the late spring 1989 (December) and in the late autumn 1990 (June). In 1989, due to an exceptional drought, no flooding was registered. Yet, four weeks before the second sampling occasion, both stands were flooded for a period of one week.

In both stands, soil organic horizons were sampled systematically (sensu TAYLOR *et al.*, 1984): within each stand 10 sampling points with a spacing of 10 m were laid out and marked along a line parallel to the river; and, on both sampling occasions, one sample was collected at each sampling point. In the forest stand, litter habitat samples (layers Ol + Of; 15 cm x 15 cm) were separated from humus habitat samples (AhI layer; 19 cm² x 5 cm) whereas, in the grassland stand, surface samples (layers Ol + Ah; 19 cm² x 5 cm) were collected. Note that no attempt was made to investigate oribatid populations during the flooding.

After extraction using BERLESE-TULLGREN funnels (4 weeks without light and heat), adult oribatids were sorted into species, when possible, and immatures were numbered globally. To compare oribatid assemblages (numerical structure), SHANNON-WIENER indices (H') (KREBS, 1989) and Bull. Annis Soc. r. belge Ent. 130, 1994

Gower similarity indices (this index responds to both species numbers and relative abundance; see LEGENDRE & LEGENDRE, 1984, for details) were calculated after data transformation into percentages.



Fig. 1. Aerial representation of the study site showing both sampled areas (1: forest stand; 2: grassland stand) near the Rio Negro river (RN), with its location in the centre of the Sedimentary Undulating region in Uruguay (F: forest; Ff: flooded part of the forest; G: grassland; Gf: flooded part of the grassland; L: Laguna Blanca pond; ts: temporary stream).

Results

Richness and density

Up to date, 31 species are definitely identified from a total of more than 50 taxa registered in the two sampling stands (see Table 1 and annotations 1 and 2 at the end of the paper). Our knowledge of the geographic distribution of these species may be summarized as follows: 28 species are known from the Neotropical region only, but their distribution is quite heterogeneous (they are typed in bold in Table 1; see also annotation 1); before our present work, one species, *Rostrozetes foveolatus*, seemed to be restricted to the Tropical regions; one species, *Galumna flabellifera*, reveals a rather remarkable distribution (South-America, Oceania, Japan); and

60

61

finally, one species, Nothrus biciliatus, is apparently cosmopolitan (BA-LOGH & BALOGH, 1988).

In terms of species richness, the number of taxa we found in the forest (>45) was within the range of maximum-minimum numbers observed in other forests in the world (i.e. between 20-60 species; WALLWORK, 1983). In the grassland, oribatid richness (<15) appeared to be lower than the one registered in two other prairies floristically more diverse (>20 species; SARASOLA, unpublished data), but was within the range recorded for grassland ecosystems in temperate oceanic climates: i.e. from 6 species in Central Ireland (CURRY & MOMEN, 1988) to 58 species in northern Spain (ITURRONDOBEITIA BILBAO & SALONA BORDAS, 1990).

The total numbers of individuals recorded on the two sampling occasions were as follows: in the forest, 4,857 adults and 1,325 immatures in spring, and 4,018 adults and 558 immatures in autumn; in the grassland, 205 adults and 16 immatures in spring, and 63 adults and 4 immatures in autumn.

On the other hand, overall mean numbers of oribatids were clearly higher in the forest (42,090 m⁻² in spring; 45,940 m⁻² in autumn) than in the grassland (11,210 m⁻² in spring; 3,410 m⁻² in autumn), but these density values are lower than those published for forest and grassland ecosystems in temperate climates (see data in WALLWORK, 1970, and LEBRUN, 1971). Moreover, in the grassland, the density of both adults and immatures decreased substantially in autumn whereas, in the forest, only the number of immatures declined significantly. Finally, in the forest, the overall abundance of oribatids in the humus habitat (22,465 m⁻² in spring; $30,770 \text{ m}^2$ in autumn) was always higher than in the litter habitat (19,625) m^2 in spring; 15,170 m^2 in autumn).

Numerical structure

This analytical part focused on taxa which defined much of the numerical structure of assemblages studied. Operationally these were taxa showed a relative abundance >1.0% (data in Table 1).

With the exception of three species (Aeroppia nasalis, Brachioppia sp. and Rioppia nodulifera) the other Oppioidea (sensu BALOGH, 1972) were numbered globally (see annotation 2). In the humus habitat of the forest, the Oppioidea dominated numerically on both sampling occasions whereas six species showed clear changes of abundance: two (Lohmannia lanceolata and Rioppia nodulifera) were substantially more abundant (relatively) in spring than in autumn whereas the reverse was registered, but less conspicuously, in Tectocepheus ssp., Epilohmannia pallida americana, Phereliodes sp. and Phyllhermannia tuberculata. These changes did not alter significantly the diversity of the humus assemblage (H' = 2.45 both in spring and autumn), but the distribution of individuals over the species was not strictly identical on both seasons (Fig. 2).

		Forest litter	litter			Forest	Forest humus			Grassland	pur	
	S	Spring	Алћ	Autumn	Spi	Spring	Au	Autumn	Spring	gu	Autum	đ
n	4	(0.1)	58	0.7)	2	(1.5)	4	(0.6)	59) 1		9	
Beneseteres organizationaes practical de manomenta 1791			34	(0.1)	4		11	(1.8)	a.		4	
Brachioppid Sp.	936	(21.2)	529	(15.5)	4	(1.0)	6	(1.5)	r			(1.5)
Controbates sputnatures DALAND as MANING 1981	53	(1.2)	21	(0.6)	6	(2.0)	E.		v		3 6 0	
Cutitoriana (10) DALVAIN AL MARINA (10)			•		13	(3.0)	¢,	(1.5)	6		552	
Eputonmanna maara reconcided 1770 E-dick-could construct Ration & Maninka 1981	•		•		49	(0,11)	17	(2.8)	ŝ	(1.4)	-	(1.5)
Equinmental puesto uncertaine provide a martine provide a second providente a secondaria secondaria a	88	(2.0)	21	(0.0)	4	(0.1)	2	(1.3)	6		10	
Fremmensets strand	1		•		•		e		-	(2.0)	•	
Columna flabellifera HAMMER 1958	194	(4.4)	21	(0.0)	œ	(1.8)	17	(2.8)	£)		a l	;
Columna diwilie Perers' Nico & Baccio 1980	177	(4.0)	31	(0.9)	ŝ	(1.2)	'n	(0.5)			-	(1.5)
CURRENT SURVEY RALDER & MANDER 1981	574	(13.0)	666	(19.5)	4	(0.1)	13	(2.1)	e e e		a j	-
Hemileius summericanus Hammer 1958	١		٢		,		j:		88	(0,04)	ŝ	(50.0)
Honloohthimaarus incredibilis (NEDBALA 1982)	35	(0.8)	92	(2.7)	3		r,		æ		9	
Liacaridae (gen. sp.)			48	(1.4)	•		ŀ:		×		э.)	
Lohmannia lanceolata GRANDIEAN 1950			,		-	(0.2)	18	(3.0)	• •	2		
Meristacarus sp.	•		• ;	1		é	8	10 00	4	(n.2)	(:)	
Nothrus biciliatus C.L. KocH 1841	35	(0.8)	82	(2-4)	4 0	(0.9)	200	(6.0)	' =	10 21	· •	(0.6)
Oppioidea (div. gen.)	203	(4.6)	171	(n·c)	007	(n-4c)	201	(n-40)	1		8	
Oribatella sp.	' ;		, ,,		¢				- 32	(0)	2	
Peloribales perteti MAHUNKA 1984	12	(0.0)	02	(4.4)	• •		•		3		2	
Pergalumna sp.	<u></u>	(c.c)	60	(0.0)	ŧ	(c'n)	20				a	
Pergalumna plumata PÉREZ-ĨÑIGO & BAGGIO 1986	2.07	(7.1)	10	(4.0)	1	10.01	v	0.0	3		29	
Pheroliodes sp.	334	(0.01)	104	(0.4)	2 2		2		29		22	
Phyllhermannia tuberculata COVARRUBIAS 1967	(C)	(1-)1)	174	(0.21)	2	(). +	2)	2		2	
Platynothrus robustior (BERLESE 1916)	77.	(c.0)	1	(0.1)	,		i a	0.10	69		9	
Rioppia nodulifera Balogh & Mahunka 1977	•		11	(c.0)	1 4	ć,	8 7	(0.11)	• •	10 002	0	000
Rostrozetes foveolatus Sellnick 1925	177	(4.0)	253	(1.4)	σ.	(n-z)	74	(4.0)	} ,	(s.uz)	0	5
	67	(2.2)	68	(2.6)	4	(1.0)	9	1	4	(n-1)	: :	ę
Tertorenheus son.	172	(3.9)	307	(0.6)	18	(9.0)	ŝ	(0.9)	Ē	((14.5)	4	(0.12)
Tectorihotes arnatus (SCHUSTER 1958)	-		,		,		ž		16	(0.7)	m	Ċ
Yewilluc contentus BALOGH & MAHUNKA 1977	6	(6.0)	34	(0.1)	'		ľ		•	9	2	
Pussibutis transfirents MAUDINEA 1985	'						•		Ξ	(0·c)	2	

62

63



Fig. 2. Cluster analysis of oribatid assemblages living in the three habitats studied, on both sampling occasions. Similarity is measured using GOWER's index and clustering is performed using the group-average sorting linkage method (see LEGENDRE & LEGENDRE, 1984).

In the litter habitat of the forest, higher values of diversity measured on both sampling occasions (3.65 in spring and 3.85 in autumn) were an indication of a greater homogeneity in the distribution of individuals over species than the one registered in the humus. However, changes of abundance which occurred in taxa, and mainly in numerically dominant taxa (i.e. *Ceratobates spathulatus*, *Phyllermannia tuberculata*, *Guaranozetes nudus*), were substantially marked with the result that the similarity between the litter assemblage on both sampling occasions showed the lowest value we measured (Fig. 2).

On the other hand, the weak similarity measured between both litter and humus assemblages is not only due to difference in species composition (9 taxa from a total of 26 inhabit only one of the two habitats). As usually observed in forest organic horizons, the numerical structure of oribatid populations living in upper layers is quite distinct from the one of populations established in lower layers (see examples in MITCHELL, 1978, WAU-THY et al., 1989, and discussion by USHER & BOOTH, 1986).

Despite the numerical dominance of *Hemileius suramericanus*, the oribatid assemblage of the grassland showed a conspicuous shift of its diversity between spring and autumn (2.60 vs 2.16, respectively). Yet, the similarity between both seasons still was markedly high (Fig. 2). Although *Hemileius suramericanus* did not inhabit the forest stand surveyed, there is evidence for numerical similarity between the oribatid assemblage living in upper organic horizons of the grassland and the one found in lower horizons of the forest. Indeed, the grassland shared seven taxa out of 13 which were also found in the forest: two (*Rostrozetes foveolatus* and *Tectocepheus* spp.) were relatively more abundant in the grassland than in the forest whereas three others (mainly Oppioidea and, to a lesser degree, Ceratobates spathulatus and Epilohmannia pallida americana) were clearly less numerous. This issue and more precisely the determinants of this similarity will be expanded in forthcoming studies.

Discussion

What is most striking in the results here reported is the weak density shown by oribatid populations and the low number of South American genera involved in the assemblages surveyed. In this discussion, we will propose some explanations for these two apparent gaps.

Density

As a general rule, alluvial soils are known to possess high fertility cycles due to lower litter C/N ratios, high biomass production, and fast rates of litter decomposition (MITSCH & GROSSELINK, 1986). Where such ecosystem characteristics are observed, and for reasons not yet fully elucidated (but biotic as well as abiotic factors are certainly involved; see a discussion by ELLIOTT *et al.*, 1980, and PONGE *et al.*, 1986), oribatid mites as well as collembolans usually show relatively weak abundances (MADGE, 1969; MCBRAYER *et al.*, 1977).

In the observed populations, it is likely that flooding has the effect of decreasing numbers which adds to the numerical depletion indicated above. Indeed, in assemblages living in Australian rainforests, HOLT (1981) has reported a drastic decrease in abundance due to flooding whereas CEPEDA & WHITFORD (1989) have pointed out that in a desert watershed flooding would have caused high mortality in immature populations. Yet, in Central Amazonian forests, BECK (1972) has highlighted four distinct types of behavior depicted by oribatid populations facing disturbances due to flooding (see also TAMM, 1984).

Consequently, it seems customary, first, to study oribatid populations during flooding phases, second, to analyse the composition and numerical structure of a greater number of assemblages experiencing flooding, and third, to compare these assemblages to others located close by but never submerged. This work is in progress. Yet, although we lack data on oribatid populations just before the flooding period (our survey was achieved six months before the flooding), our results suggest two hypotheses, as follows :

Hypothesis 1

Flooding could be regarded as a "type I" perturbation (sensu SUTHER-LAND, 1981) which has little effect on the composition and numerical structure of oribatid assemblages (i.e. to which assemblages are resistant). An argument in support of this hypothesis is the fact that no clear differences in the pattern of numerical dominances were observed between the two sampling occasions. Indeed, in the forest, *Ceratobates spathulatus*, *Phyllhermannia tuberculata* and *Guaranozetes nudus* were numerically dominant

IN AUTUMN

66

within the litter habitat both in December and in June; so were the Oppioidea within the humus habitat, and *Hemileius suramericanus*, *Rostrozetes foveolatus* and *Tectocepheus* spp. in the grassland (Table 1). This suggests that the deviations of similarity measured for the assemblages would only be due to intrinsic, normal fluctuations of population sizes (see e.g. MIT-CHELL, 1979).

Hypothesis 2

If flooding was a major disturbance (i.e. a "type II" perturbation, sensu SUTHERLAND, 1981) acting, for example, on immature populations as postulated by HOLT (1981) and CEPEDA & WHITFORD (1989), the resilience (sensu HOLLING, 1973) of oribatid assemblages would seem to be higher in grassland than in forest as illustrated in fig. 2. To test this hypothesis, our future field observations will try to find out, for example, whether age-specific mortality and fecundity rates are similar or not in both flooded and unflooded biotopes, with the purpose to assess whether flooding is a mechanism, the effects of which have produced or produce the maintenance of diversity of oribatid assemblages.

South American genera

In the study site, we found eight genera (i.e. Aeroppia, Amazoppia, Baloghacarus, Berlesezetes, Ceratobates, Frondoppuia, Guaranozetes and Rioppia) whose range is confined to South America, from a total of more than 85 genera (HAMMER & WALLWORK, 1979). Although, on all continents, the number of species and consequently the number of genera tend to decrease with increasing distance north or south from the equator (see e.g. PIANKA, 1966), the number of South American genera we detected appears to be relatively low.

A possible explanation for this weakness could be found in the pattern of geographical dispersal shown by many if not all the species. Indeed, a commonly accepted biogeographic principle is that a species tends to be less abundant, even in its preferred habitat, towards the edge of its distribution (BROWN, 1984). And so, and regardless of the underlying mechanisms (but see RICKLEFS, 1987), this gives rise to areas depauperate in species where many species' range limits coincide (CODY, 1975).

It could be then hypothesized that, in the Pampas region (sensu Good, 1964), oribatid species of the South Brazilian region reach their southern, distributional limits, and that similarly species of the Andean region and of the Patagonian region reach their eastern and northern limits respectively, resulting in a decline in species number.

A better knowledge of the distribution of South-American oribatid mites and also of their endemism and niche breadth is imperatively required to confirm this hypothesis. Yet, two observations available to date strengthen the biogeographical explanation we propose: (1) from data in BALOGH & BALOGH (1988, 1990) and PÉREZ-IÑIGO & BAGGIO (1980), it seems that two Bull. Annls Soc. r. belge Ent. 130, 1994

species we found in the study site (i.e. *Platynothrus robustior* and *Epiloh-mannia maurii*) are widespread only in the Pampas region whereas all the other taxa (at least the ones identified for sure to species) show a wider distribution; (2) from the report by CHEBATAROFF (1950) on tropical plants which are widely distributed (south of Brazil, Paraguay and north of Argentina), but reach their eastern limits in Uruguay, one can predict that several oribatids find likewise their distributional limits in Uruguay, if we assume however that plant and animal distributions similarly converge.

Annotations

1. In the forest stand, 12 taxa were found either in the litter habitat (L) or in both the litter and humus habitats (O), but with a relative abundance <1.0%. Several of these taxa are only known from the Neotropical region, i.e.: Aeroppia nasalis MAHUNKA, 1985 (L), Amazoppia tricuspidiata BALOGH & MAHUNKA, 1981 (L), Baloghacarus australis BALOGH & MAHUN-KA, 1981 (L), Carabodes atrichosus MAHUNKA, 1984 (L), Microtegeus quadristriatus MAHUNKA, 1984 (L), Nanhermannia elegantissima HAMMER, 1958 (L), Nothrus becki BALOGH & MAHUNKA, 1981 (O), Rhysotritia brasiliana MAHUNKA, 1983 (L) and Xenillus brasilianus BALOGH & MAHUNKA, 1969 (L), whereas the following ones cannot be linked for sure to a known species: Eremulus sp. (O), Miracarus sp. (O), Orthogalumna sp. (L) and Phthiracarus sp. (L).

2. The determination of Oppioidea (sensu BALOGH, 1972) is very difficult because diagnoses are usually too short or too imprecise. Yet, the majority of individuals found in the study site could be linked to the following genera: Aeroppia HAMMER, 1961, Frondoppia MAHUNKA, 1983, Microppia BALOGH, 1983, Moritziella BALOGH, 1983, Oxyoppia BALOGH & MAHUNKA, 1969, Rectoppia SUBIAS, 1980 and Teratoppia BALOGH, 1959. The study of morphological traits shown by immatures is required to link for sure these genera to the family Oppiidae GRANDJEAN, 1953. On the other hand, the other oppioids, less numerous than previous ones, could be related to three species belonging to the Suctobelbidae.

Acknowledgements

This study was supported by PEDECIBA funds. Thanks are extended to Mr R.D. KIME for reviewing our english manuscript. Thanks are also due to Mrs G. BORRAS, Mrs G. BOCAGE, Mrs M. VAN ASSCHE and Mr H. VAN PAESSCHEN for their valuable assistance.

References

- BALOGH, J., 1972. The Oribatid Genera of the World. Academiai Kiado, Budapest, 188 pp.
- BALOGH, J. & BALOGH, P., 1988. Oribatid Mites of the Neotropical Region. 1. Elsevier, Amsterdam, 335 pp.

67

- BALOGH, J. & BALOGH, P., 1990. Oribatid Mites of the Neotropical Region. 2. Elsevier, Amsterdam, 332 pp.
- BECK, L., 1972. Der Einfluss der jahresperiodischen Überflutungen auf den Massenwechsel der Bodenarthropoden im zentral-amazonischen Regenwaldgebiet. Pedobiologia, 12: 133-148.
- BROWN, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat., 124: 255-279.
- CARRERE, R., 1989. Desarrollo Forestal y Medio Ambiente en el Uruguay, 2. El Bosque Natural Uruguayo: Caracterizacion General y Estudios de Casos. Ciedur, Montevideo, 105 pp.
- CEPEDA-PIZARRO, J.G. & WHITFORD, W.G., 1989. Spatial and temporal variability of higher microarthropod taxa along a transect in a northern Chihuahuan Desert watershed. Pedobiologia, 33: 101-111.
- CHEBATAROFF, J., 1950 Algunos aspectos evolutivos de la vegetación de la provincia fitogeográfica uruguayense. Revta nac., 201: 406-421.
- CODY, M.L., 1975. Towards a theory of continental species diversities: Bird distributions over Mediterranean habitat gradients, pp. 214-257. In: CODY, M.L. & DIAMOND, J.M., (eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts, 545 pp.
- CURRY, J.P. & MOMEN, F.M., 1988. The arthropod fauna of grassland on reclaimed cutway peat in Central Ireland. Pedobiologia, 32: 99-109.
- DELECOUR, F., 1980. Essai de classification pratique des humus. Pédologie, 30: 225-241.
- DURAN, A., 1985. Los Suelos del Uruguay. Hemisferio Sur, Montevideo, 398 pp.
- ELLIOTT, E.T., ANDERSON, R.V., COLEMAN, D.C. & COLE, C.V., 1980. -Habitable pore space and microbial trophic interactions. Oikos, 35: 327-335.
- GOOD, R., 1964. The Geography of Flowering Plants. 3rd ed. Longmans. London, 518 pp.
- HAMMER, M. & WALLWORK, J.A., 1979. A review of the world distribution of oribatid mites (Acari: Cryptostigmata) in relation to continental drift. Biol. Skr., 22 (4): 1-31.
- HOLLING, C.S., 1973. Resilience and stability of ecological systems. A. Rev. Ecol. Syst., 4: 1-23.
- HOLT, J. A., 1981. Acari and Collembola in the litter and soil of three north Qeensland rainforests. Aust. J. Ec., 10: 57-65.
- ITURRONDOBEITIA BILBAO, J.C. & SALONA BORDAS, M., 1990. Estudio de las comunidades de oribátidos (Acari: Oribatei) de varios ecosistemas de Vizcaya y una zona próxima. 2. Distribución de abundancias y diversidad específica. Revue Ecol. Biol. Sol, 27: 113-133.
- KREBS, J.C., 1989. Ecological Methodology. Harper & Row, New York, 654 pp.
- LEBRUN, Ph., 1971. Écologie et biocénotique de quelques peuplements d'arthropodes édaphiques. Mém. Inst. r. Sci. nat. Belg., 165: 1-203.
- LEGENDRE, L. & LEGENDRE, P., 1984 Écologie Numérique, 2. La Structure des Données Écologiques. Masson, Paris, 335 pp.

- MADGE, D.S., 1969. Litter disappearance in forest and savanna. Pedobiologia, 9: 288-299.
- MCBRAYER, J.F., FERRIS, J.M., METZ, L.J., GIST, C.S., CORNABY, B.W., KITAZANA, Y., KITAZANA, T., WERNA, J.G., KRANTZ, G.N. & JENSEN, H., 1977. - Decomposer invertebrate populations in U.S. forest biomes. Pedobiologia, 17: 89-96.
- MITCHELL, M.J., 1978. Vertical and horizontal distributions of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. Ecology, 59: 516-525.
- MITCHELL, M.J., 1979. Effects of physical parameters and food ressources on oribatid mites in forest soils, pp. 585-592. In: RODRIGUEZ, G., (ed.), Recent Advances in Acarology, Vol. 1. Academic Press, New York. 631 pp.
- MITSCH, W.J. & GROSSELINK, J.G., 1986. Wetlands. Van Nostrand Reinhold, New York, 539 pp.
- PÉREZ-INIGO, C. & BAGGIO, D., 1980. Oribatidos edáficos do Brasil. Bolm. Zool. Univ. S. Paulo, 5: 111-117.
- PIANKA, E.R., 1966. Latitudinal gradients in species diversity: A review of concepts. Am. Nat., 100: 33-46.
- PONGE, J.-F., VANNIER, G., ARPIN, P. & DAVID, J.-F., 1986. Caractérisation des humus et des litières par la faune du sol. Intérêt sylvicole. Revue forest. fr., 38: 509-516.
- RICKLEFS, R.E., 1987. Community diversity: Relative roles of local and regional processes. Science, 235: 167-171.
- SUTHERLAND, J.P., 1981. The fouling community at Beaufort, North Carolina: A study in stability. Am. Nat., 118: 499-519.
- TAMM, J.C., 1984. Surviving long submergence in the egg stage: A successfull stategy of terrestrial arthropods living on flood plains (Collembola, Acari, Diptera). Oecologia (Berlin) 61: 417-419.
- TAYLOR, J.A., FRIEND, G.R. & DUDZINSKI, M.L., 1984. Influence of sampling strategy on the relationships between fauna and vegetation structure, plant lifeform and floristics. Aust. J. Ecol., 9: 281-287.
- USHER, M.B. & BOOTH, R.G., 1986. Arthropod communities in a marine antarctic moss-turf habitat: Three-dimensional distribution of mites and Collembola. J. anim. Ecol., 53: 427-441.
- WALLWORK, J.A., 1970. Ecology of Soil Animals. McGraw-Hill, London, 283 pp.
- WALLWORK, J.A., 1983. Oribatids in forest ecosystems. A. Rev. Ent., 28: 109-130.
- WAUTHY, G., NOTI, M.-I. & DUFRÊNE, M., 1989. Geographic ecology of oribatid mites in deciduous forests. Pedobiologia, 33: 399-416.